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Organization of Afrotropical plant-bird pollination communities: the effects of altitude and seasonality

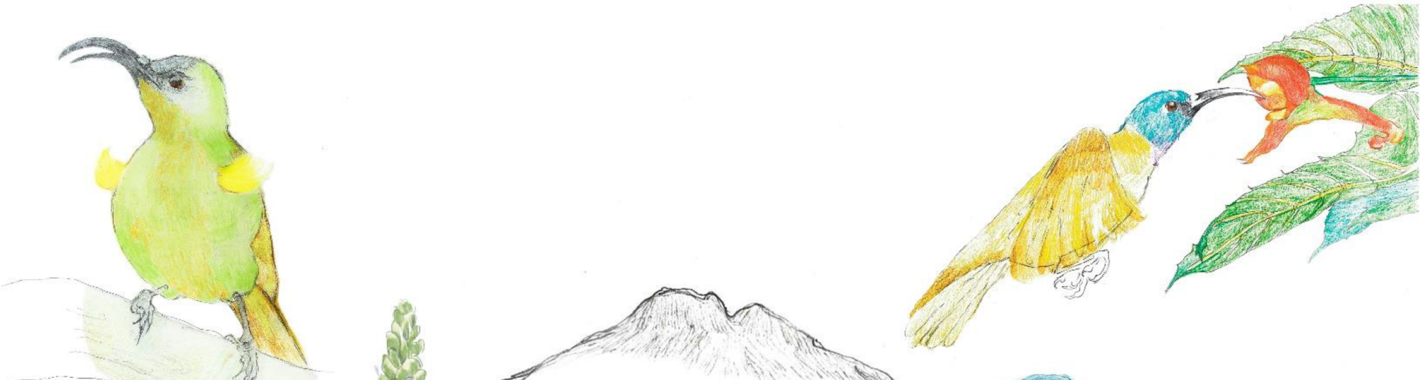
Organizace afrotropických společenstev rostlin a jejích ptačích opylovačů

Doctoral dissertation

Supervisor: Mgr. Štěpán Janeček, Ph.D.

Advisor: David Hořak, Ph.D.

Prague, 2024



DECLARATION OF ORIGINALITY

I declare that this dissertation has not been submitted for the purpose of obtaining the same or another academic degree earlier or at another institution. My involvement in the research presented in this thesis is expressed through the authorship of the included manuscripts and publications. All literature sources used when writing this thesis have been properly cited.

Prague, 26.08.2024

Prohlašuji, že jsem závěrečnou práci zpracoval samostatně a že jsem uvedl všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

V Praze, 26.08.2024

Guillermo Uceda Gómez, M.Sc.

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STATEMENT OF CONTRIBUTION

I declare that the research found in this thesis was conducted in collaboration with Czech and international scientists. My personal contribution to the conception, data collection, curation, analysis, and manuscript writing for each of the following chapters is truthfully described in the “Chapters and author’s contributions” section.

Prague, 26.08.2024

Guillermo Uceda Gómez, M.Sc.

As a supervisor of this doctoral thesis and co-author of all included papers and manuscripts, I declare that the contribution of the Ph.D. student, Guillermo Uceda Gómez, to the published, submitted and finished manuscripts can be considered more than sufficient to justify the inclusion of the papers in this Ph.D. dissertation.

Prague, 26.08.2024

Mgr. Štěpán Janeček, Ph.D.

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CHAPTERS AND AUTHOR'S CONTRIBUTIONS

This desertion comprises the following papers and the role of the candidate has been described below and summarised in Table 1.

PART-I DRIVERS OF SUNBIRD-PLANT POLLINATION INTERACTIONS

Chapter I

Uceda-Gómez, G., Chmel, K., Janečková, P., Mlíkovský, J., Klomberg, Y., Ewome, F. L., Molua, L. L., Njie, M. M., Tropek, R., & Janeček, Š. (2024). Drivers of sunbird-plant interactions on Mount Cameroon: Between neutrality and niche-based processes. *Biotropica*, 56, 136–148. https://doi.org/10.1111/btp.13290

GUG was highly involved in the conceptualisation of this study, sampling of field data and their processing; he oversaw all analyses, and their interpretations. First versions of this manuscript were written by GUG under the supervision of ŠJ.

PART-II BIRD POLLINATION SYNDROME CONCEPT

Chapter II

Janeček, Š., Chmel, K., **Uceda Gómez, G.**, Janečková, P., Chmelová, E., Sejfová, S., & Ewome, F.L. (2020). Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution*, 10, 1784–1793. https://doi.org/10.1002/ece3.5942

GUG performed all the laboratory procedures involving the staining and counting of pollen tubes under fluorescence microscopy. He also took microscopic pictures of the pollen tubes. Additionally, he also contributed to the editing of the manuscript.

Chapter III

Mundi, O., Awa II, T., Chmel, K., Ewome, F.L., **Uceda-Gómez, G.**, Janečková, P., & Janeček, Š. (2022). The ornithophily of *Impatiens sakeriana* does not guarantee a preference by sunbirds. *Biological Journal of the Linnean Society*, 137, 240-249. https://doi.org/10.1093/biolinnean/blac083

GUG was strongly involved in the fieldwork conducting the cage experiments in collaboration with the team. GUG also analysed the video material of bird floral preferences. Additionally, he also contributed to the editing of the manuscript.

Chapter IV

Chmel, K., Ewome, F.L., **Uceda Gómez, G.**, Klomberg, Y., Mertens, J.E.J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome works as the plant's adaptation to ornithophily, while nectarivorous birds do not seem to care. *Oikos*, 130, 1411-1424. https://doi.org/10.1111/oik.08052

GUG was strongly involved in the fieldwork, participating in the acquisition of the bird dataset. Additionally, he also contributed to the editing of the manuscript.

PART-III SPATIOTEMPORAL VARIABILITY IN SUNBIRD-PLANT POLLINATION INTERACTIONS

Chapter V

Janeček, Š., **Uceda-Gómez, G.**, Janečková, P., Tropek, R., Fominka, N.T., Njie, M.M., Mlíkovský, J., Kamga, S.M., Molua, L.L., & Ewome, F.L. (2024). Food resource partitioning between males and females of Volcano Sunbird *Cinnyris preussi* on Mount Cameroon. *Journal of Ornithology*, *https://doi.org/10.1007/s10336-024-02187-8*

GUG was strongly involved in data collection both in the forest elevational gradient and the grasslands. He helped to conceptualize the study and helped to raise funds necessary to conduct it. Additionally, he also contributed to the editing of the manuscript and contributed to the supplementary materials with figure and/or tables.

Chapter VI

Janeček, Š., Chmel, K., Mlíkovský, J., **Uceda-Gomez, G.**, Janečková, P., Fominka, N.T., Njie, M.M., & Ewome, F.L. (2022). Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. *Oecologia*, 199, 885-896. https://doi.org/10.1007/s00442-022-05234-4

GUG was strongly involved in the fieldwork, participating in the acquisition of the sunbird-plant interaction dataset, as well as the plant abundance dataset. Additionally, he also contributed to the editing of the manuscript.

Chapter VII

Uceda-Gomez, G., Molua, L.L., Mani, F.T., Ewome, F.L., & Janeček, Š. (manuscript under review; Journal of Plant Ecology) Coping with altitude: Altitude-driven visitor shifts to *Hypericum revolutum* (Hypericaceae) on Mount Cameroon grasslands.

GUG together with LLM collected the data. GUG together with ŠJ conceptualized the study. GUG raised the funds necessary to conduct the study. GUG analysed the dataset and wrote the manuscript under the supervision of ŠJ.

Table 1. List of chapters included in this doctoral thesis and the contribution of the author to each of them. The different colours depict the two main overarching topics of this dissertation namely: trait-matching and niche-based processes (in light blue) and bird-plant interactions across elevational gradients (in dark blue). Notice, chapter V is depicted as a colour in between the other two as it encompasses both topics and serves as a hinge between them both.

	Contribution							
Chapter	**Design**	**Fieldwork**	**Data processing**	**Data analyses**	**Lab work**	**Figure/table preparation**	**Manuscript preparation**	**Manuscript editing/reviewing**
I	**X**	**X**	**X**	**X**	**NA**	**X**	**X**	**X**
II					**X**			**X**
III		**X**	**X**		**NA**			**X**
IV		**X**			**NA**			**X**
V	**X**	**X**			**NA**	**X**		**X**
VI		**X**			**NA**			**X**
VII	**X**	**X**	**X**	**X**	**NA**	**X**	**X**	**X**

PREFACE AND ACKNOWLEDGEMENTS

Ever since I was a child, I have been fascinated by the animal world. I remember a trip I took with my family to Argentina as one of the reasons that made me decide to become a biologist. There, at Iguazu Falls National Park, I remember seeing toucans and being mesmerized by the beauty of the tropical forest. My journey as a biologist started in 2009 at the Autonomous University of Madrid. Little by little I became interested in the fields of evolution, zoology and ecology. Nevertheless, the path to this thesis has not been straight. I have been in involved in several fields as I have taken courses, on palaeontology, animal behaviour, and anthropology. My bachelor's culminated with a thesis on the antipredator behaviour of wild and domestic ungulates. This was my first contact with research. After finishing my bachelor, I moved to The Netherlands where I narrowed down my interest. During these years, I discovered that what I liked the most was doing fieldwork. Thus, I had the opportunity to join an expedition to the Russian arctic to study migratory geese. As you can see, for me botany-related studies were never a choice but this PhD. has changed my mind.

First, I would like to thank my PhD. supervisor Štěpán Janeček who made it possible for me to study bird pollination in Cameroon and transmitted to me his passion for Afrotropical research. Further, I would like to thank David Hořak for helping me to settle down in the university by providing me with a nice working space and environment and allowing me to teach. Moreover, I would like to thank Robert Tropek that despite not being my supervisor he has taught me a lot during these years. Additionally, I would like to thank Kryštof Chmel and Jiří Mlíkovský for teaching everything they know about ornithology. Also, I would like to thank Natasha Louise de Vere, Brandon Samuel Whitley, and Zhao Li for warmly welcoming me in Copenhagen and for teaching me the ways of metabarcoding.

Second, I would like to thank our Cameroonian collaborators from whom I have learnt a lot, and for giving me a warm welcome in Bokwango. Thus, Francis "Escobar" Luma, Francis Teke Mani, his royal highness Nestoral T. Fominka, Markus Mokake Njie, Eko Mwende, Marcus Ngotto, John Ngotto, Peter Abieja, Rodulf Mokake, and Klaus Elive; thank you very much. I am grateful for the hours we spend together in the field and without your help we would not have been able to perform our research on Mount Cameroon (Fig. 1). Special thanks go to Lucas Lyonga Molua, as he likes to say, *"my brother from another mother"*. We have spent countless hours hiking Mt. Cameroon and catching birds together. "*Lions never surrender my friend"*.

I could not go without thanking my fellow PhD. students at the department. Special thanks go to Sailee Shakhalkar for always answering my, sometimes annoying, questions and for encouraging me to go on Erasmus. Also thank you for the nice silhouettes of the sunbirds that you drew for my first paper. Sorry for not pronouncing your name properly. Lately, I am making an effort to do it correctly. Thanks to Javier Oñate Casado, and Riccardo Pernice (a.k.a. Chavallo or Mr. Pernice) for the coffees and cigarettes we have had together talking about our respective projects. You three are not only my colleagues but also my friends. I hope to work with you in the future. Thanks as well to Antigone Sounapoglu for being my very good friend these years in Prague, I hope your PhD. journey comes to an end soon. Moreover, thanks to Yannick Klomberg for welcoming in Prague, and for being the nice guy that he is. I would also like to thank Fernando Gaona (a.k.a. Feno), Dominik Anýž, Jan Filip, and Tereza Kočárková for creating a nice environment in the office.

I also want to express my gratitude to my friends back home for always welcoming me with open arms. Thanks to "Tito", Nuria, "Patxi", "Apa", "Jagger", "Lottox", Rafa, and all the *"el parque"* community with whom I have spent countless hours. Special thanks to Sandra García González for being one of my best friends and for spending some of her time drawing the birds for this thesis. In the friends chapter, I have a special place for my mate Mario Martínez Monleón. Ever since we started the bachelor together, we have been very good friends. We have spent countless hours among beers, discussing evolution, or listening to our favourite music genre, Reggae. *"Jah bless my friend, One Love"*. Also thank you to my friends in Prague: Paco, Dani, Jagoda, Viktor; Emily; Tomaš, and Venca.

Finally, I would like to thank my family. My father Javier for being a source of inspiration. My mum Maria Eugenia for always supporting me. My brother Pablo for being a role model from whom I learnt a lot. Also, special thanks to my girlfriend, Hazal, who despite entering my life not so long ago has been a constant source of support. She is my number one supporter, who has taught me not to undermine myself. I hope this new chapter of our lives, brings us to a better place, and we grow together as better people.

Figure 1. Moments at Mount Cameroon. A) Me and Lucas Lyonga Molua during a break from our observations of bird visitors on *Hypericum revolutum* on the montane grasslands. **B**) Part of the research team after our expedition during the dry season to the lowest elevations of Mount Cameroon. **C)** Improvised badminton match at Fermencam camp (1800 m a.s.l. **D)** Van ready to take us to Bakingili village from where we hiked to Drinking Garri camp (650 m a.s.l.)

ABSTRACT

The pollination syndrome concept has been a central theory in pollination research, though it is not without controversy. A key issue is that plants often attract multiple pollinator functional groups, challenging the idea of necessary coevolution with specific floral visitors. Two main mechanisms have been proposed to explain plant-pollinator interactions: *neutral processes*, where interactions are driven by the relative abundances of plants and pollinators, and *niche-based processes*, where the traits of both partners dictate the interactions. As a result, interactions may stem from forbidden links or trait-matching. Research has yielded mixed support for both neutral and niche-based processes. Furthermore, spatiotemporal variability affects species' niche breadth and niche partitioning within bird-plant networks, with elevational gradients offering valuable opportunities to test these hypotheses. This dissertation explores the validity of the bird pollination syndrome, the drivers of bird-plant interactions, and their spatiotemporal variability. Additionally, this thesis provides insights into bird-pollination systems from a relatively understudied region of the world and contributes to the understanding of the ecology of sunbirds (Nectariniidae). We highlight the significant asymmetry in sunbird-plant interactions. The bird pollination syndrome remains valid, although certain plant traits, such as corolla tube length and the amount of offered reward, appear to be more relevant than others. Sunbird-plant interactions may not be as tight as previously thought, with periods promoting the evolution of trait-matching between the partners. Likewise, ecological fitting seems sufficient to facilitate these interactions. Additionally, this dissertation has provided valuable insights into the dynamic nature of studied systems with certain structural features of sunbird-plant interaction networks, being influenced by elevation and seasonality. We demonstrate how sunbird-plant networks are as specialised as their New World counterparts, including hummingbird-plant interactions.

ABSTRAKT

Koncept polinačních syndromů, ačkoli často kontroverzní, představuje jednu z ústředních teorii ve výzkumu opylování. Hlavním problémem tohoto konceptu je především fakt, že jednotlivé druhy rostlin často lákají mnoho funkčních skupin opylovačů, což naznačuje spíše absenci koevoluce rostlin s jednotlivými návštěvníky. K vysvětlení interakcí mezi květy a návštěvníky byly navrženy dva hlavní mechanismy: neutrální procesy, kdy četnost jednotlivých interakcí je dána pouze četností jednotlivých druhů rostlin a opylovačů, a procesy založené na rozdílnosti nik jednotlivých organizmů, kdy jsou četnosti interakcí výsledkem specifických vlastností druhů. Díky těmto vlastnostem (adaptacím) organismů mohou být některé interakce zcela znemožněny (tzv. forbidden links) nebo mohou být naopak umožněny oboustranými koadaptacemi (tzv. trait-matching). Výzkum zatím přinesl podporu pro oba tyto mechanismy. Navíc v interakčních sítích je šířka nik a jejích rozdělení mezi druhy ovlivněna časoprostorovou variabilitou. Tyto vlivy lze dobře studovat podél gradientů prostředí jako například podél gradientů nadmořské výšky. Tato diplomová práce zkoumá ptačí polinační syndrom, jednotlivé mechnismy určující interakce mezi ptáky a rostlinami a jejích časoprostorovou variabilitu. Práce se zároveň zaměřuje na relativně málo probádanou oblast světa a přispívá k porozumění ekologie strdimilů (čeledi Nectariniidae). Práce odhaluje značnou asymetrii v interakcích mezi strdimily a rostlinami. Koncept polinačních syndromů se ukazuje být správný, ačkoli určité vlastnosti květů, např. délka květní trubky nebo množství nabízené odměny, se zdají být důležitější než jiné květní vlastnosti. Interakce mezi strdimily a rostlinami nemusí být tak těsné, jak se původně předpokládalo, avšak existují

1. INTRODUCTION

Before delving into what the drivers behind the observed plant-bird pollination interactions are, and the structuring of these networks, I considered necessary to have a glimpse into the natural history of angiosperms, the evolution of pollination, and the shift from insect to bird pollination. Therefore, the first sections of this thesis deal with how old flowering plants are and how animal pollination evolved. Later in my dissertation, I will deal with other important concepts that structure my thesis, namely the bird pollination syndrome, trait-matching, and ultimately the spatiotemporal variation in bird-plant interactions.

Origin of the crown group of angiosperms

Angiosperms, that is flowering plants, play a pivotal role in nearly all terrestrial and aquatic ecosystems. Therefore, knowledge of their origin and evolution provides the building blocks for understanding the history and composition of major terrestrial ecosystems and general patterns of biodiversity. Even though the exact number of species is not yet known, and more species are described every year, estimates of c. 300000 living species suggest that they account for nearly 90% of all land plants (i.e., embryophytes; Sauquet et al., 2022).

Several authors have pointed out the importance of determining the crown age of angiosperms for assessing hypotheses regarding the influence of angiosperm–insect interactions, including pollination, in facilitating the early diversification of both angiosperms and essential insect orders (Asar et al., 2022; Benton et al., 2022; Van Der Kooi & Ollerton, 2020). The crown-age estimates vary considerably among studies and methodologies applied (Sauquet et al., 2022). Magallón et al., (2015) estimated the crown-age of angiosperms as 136-139.35 Ma. They used the age of the earliest known angiosperm fossil, and the number of angiosperm families in the fossil record to give this estimation. Moreover, Silvestro et al., (2015) estimated the crown-age in the interval of 133.0-151.8 Ma. These two studies tore down the longstanding belief that the absence of pre-cretaceous angiosperms fossils made it impossible for them to have originated earlier in evolutionary history (Sauquet et al., 2022). Notably, the oldest known angiosperm fossil dates to c. 130 Ma. Additionally, Silvestro et al. (2021) also suggested an even older pre-cretaceous origin of the angiosperm crown node (153.7-254.8 Ma), emphasizing the possibility of angiosperm origin much earlier than the oldest known fossil.

Moreover, fossil-calibrated molecular studies have provided much younger estimations for the origin of modern angiosperms. In this sense, Foster et al. (2017) applied an age constraint of 139.35 Ma and gave a narrow bracket for the angiosperm origin, c. 138-139 Ma. Likewise, Barba-Montoya et al. (2018) and Ramírez-Barahona et al. (2020), estimated the crown age of angiosperms in 149-162 and 153.7-154.2 Ma, respectively. Nonetheless, these estimations were highly based on assumptions placed on the crown node of angiosperms, and thus do not represent free estimates. For instance, the same authors estimated the crown age of angiosperms to be 192–253 Ma and 206–253 Ma, respectively. Yet, these analyses were conducted without any assumptions regarding the origin of angiosperms based on the fossil record, and therefore allow for much older estimations. Other recent studies have reported similar findings (Li et al., 2019; Nie et al., 2020) or even more ancient crown age estimations (Salomo et al., 2017; Zhang et al., 2020).

Thus, there is no consensus in the scientific community about the origin of the modern angiosperms with some scientist dating their origin around the Jurassic-Cretaceous boundary and others dating it earlier in evolutionary history. Despite this controversy, all the analyses indicate that they very likely originated before the oldest known angiosperm fossil, however, how old is still a matter of debate (see Fig. 2).

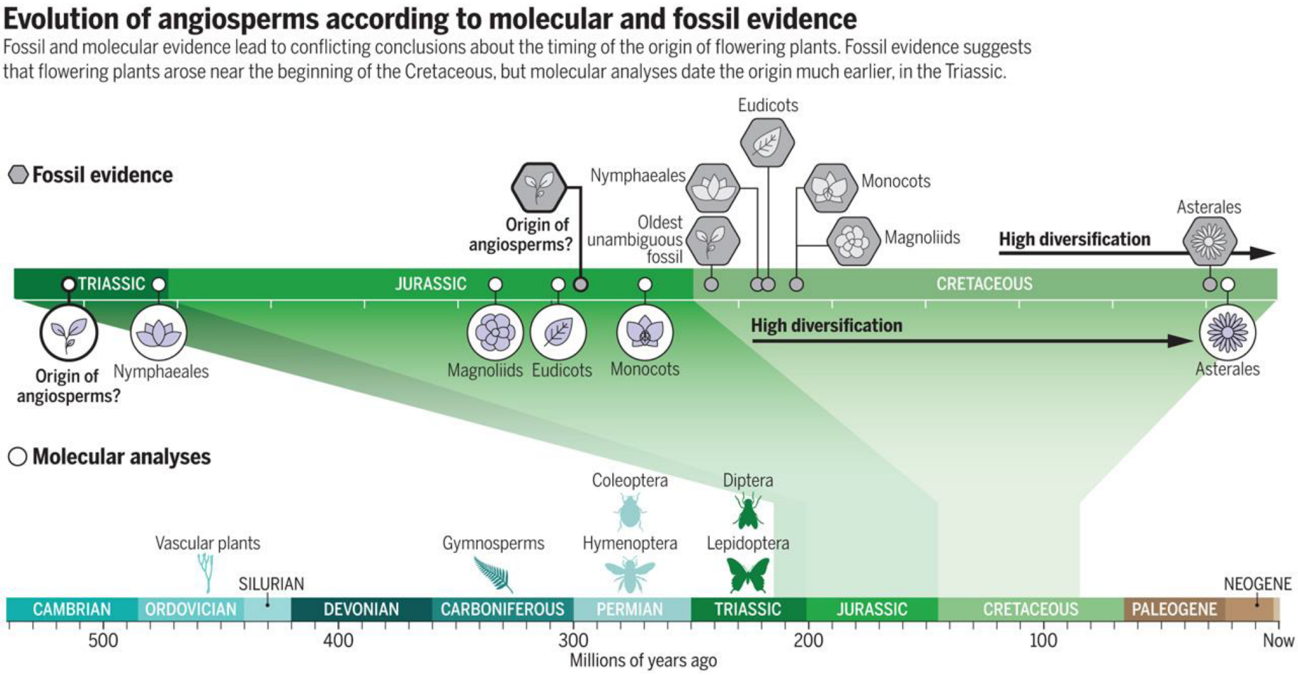

Figure 2. On the origins of angiosperms by different methodologies (i.e., fossil, and molecular dating). As shown in the figure still there is a lot of debate on the origins of angiosperms. (adapted from van der Koii & Ollerton, 2020)

Origin of animal pollination

One of the key features of angiosperms is their unique relationship with animal pollinators, especially with insects. The rapid radiation of angiosperms in a short geological period already caught the attention of Darwin who referred to it as "an abominable mystery" (Buggs, 2021). Cardinal & Danforth (2013) stated that the origin of several flower-visiting insect orders, namely Coleoptera, Diptera, Hymenoptera, and Lepidoptera, dates to the Permian or Triassic, with a period of massive radiation during the Cretaceous, coinciding with the radiation of angiosperms. During the late Cretaceous and early Paleogene (c. 50-100 Ma) the rise to dominance of Angiosperms provoked fundamental changes in the land Earth-life system (*"The Angiosperm Terrestrial Revolution";* Benton et al., 2022). Terrestrial ecosystems underwent a boost in biodiversity facilitated by key angiosperm innovations, such as the coevolution with pollinators and herbivores. Nonetheless, Asar et al. (2022) argue against the codiversification of insect and angiosperm lineages. According to these authors, there is a mismatch between the emergence and initial diversification of angiosperms and the origin and diversification of their key insect pollinators. Moreover, the fossil record evidences that these insect orders already had mutualistic relationships with gymnosperms.

Historically, the appearance of animal pollination was conceived as a transition from primitively wind-pollinated gymnosperms to more evolved animal-pollinated angiosperms. Nonetheless, this view has been proven incorrect (Ollerton, 2017). **But how this mutualism appeared?** Antagonistic interactions between plants and animals, such as the consumption of pollen by animals, may represent an initial step in the evolution of animal-mediated pollination. Earlier work from Ren et al., (2009) demonstrated that a group of Mesozoic scorpionflies fed on a nectar-like fluid from an extinct lineage of gymnosperms. These authors suggested that the flies in turn would pollinate the plant. Moreover, recent studies from various fossil sites worldwide have demonstrated the association between several groups of fossil insects and pollen grains through the analysis of their mouthparts (Labandeira, 2010; Peñalver et al., 2015). These findings shed light on the earliest forms of animal pollination. Therefore, animal pollination existed long before the emergence of angiosperms, with gymnosperms already employing insects for securing pollination.

The association between potential pollinators and gymnosperms persisted since the early Permian (283-273 Ma), preluding the first flowering plants by c. 100 Ma. The first evidence for angiosperm-insect interactions does not appear in the fossil record until the Late Cretaceous, c. 99 Ma. One potential explanation for the shift was that insects were already feeding on gymnosperm pollination drops. Therefore, by evolving nectar, angiosperms provided a more nutritious fluid, enabling host switching and accidentally securing cross-pollination among conspecifics. Stephens et al. (2023) demonstrated that insect pollination is the ancestral pollination mode for angiosperms. Likewise, Hu et al. (2008) showed that 86 % of basal angiosperm families were insect-pollinated. These results also agree with the reconstruction of the ancestral flower made by Sauquet et al. (2017). In this sense, this ancestral flower would match the floral syndrome of a generalist insect visitor.

While insects were (and still are) the primary pollinating functional group, other groups, such as vertebrates, emerged as significant pollinators over time. Understanding the role of vertebrates in pollination requires examining when they first began participating in this process. The next section will explore the origins of vertebrate pollination, with a particular emphasis on avian pollinators. Special attention will be given to hummingbirds (Trochilidae), as the most important vertebrate pollinator group. See Fig. 3 for a summary of the species diversity of the different functional groups of vertebrate pollinators.

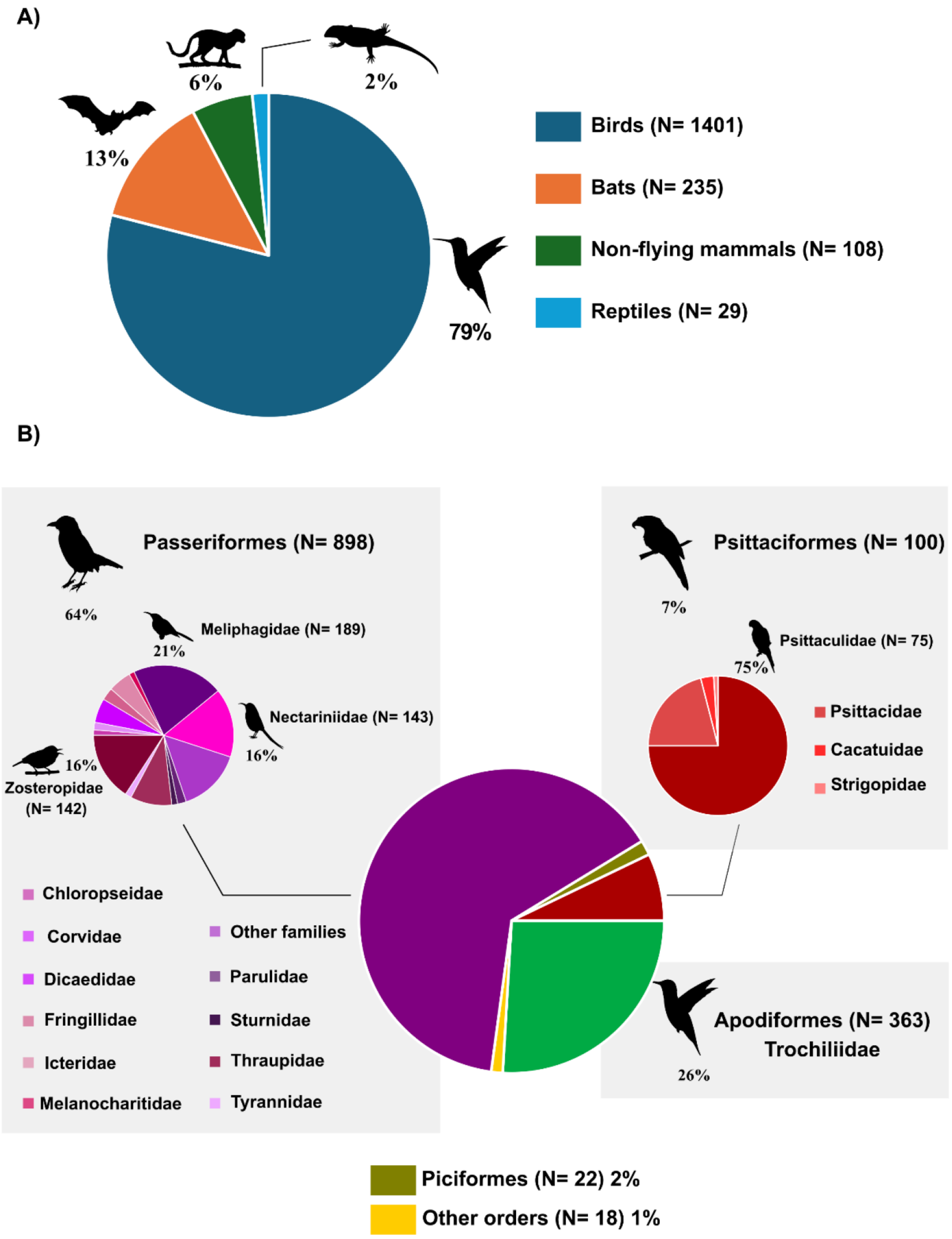

Figure 3. Diversity of vertebrate pollinators. **A)** Vertebrate pollinator diversity by functional group. Percentages represent the number of species of a particular group relative to the total number of vertebrate pollinators. **B)** Bird order diversity, highlighting key flower-visiting orders, with percentages representing species counts relative to the total number of bird flower-visiting species in each taxonomic level. Data sources: Birds (Ollerton, 2024), bats and no-flying mammals (Regan et al., 2015), and reptiles (Olesen & Valido, 2003).

Birds as pollinators. Origin and shift from insect to bird pollination

Nectarivory, or flower-visiting in a broader sense, evolved independently in three extant avian groups: Apodiformes (i.e., Trochilidae), Psittaciformes (e.g., Psittaculidae; Loriini tribe) and Passeriformes (e.g., Nectariniidae, Dicaeidae, Meliphagidae). The earliest evidence of bird pollination dates to the Early Oligocene from fossils of modern hummingbirds found in Europe (*Eurotrochilus inexpectatus*; Mayr, 2004). Honeyeaters (Meliphagidae) and Psittaciformes are represented in the fossil record, with some fossils from the Miocene in Australia and New Zealand (Boles, 2005; Worthy et al., 2011). The phylogenies of Nectariniidae and Meliphagidae are not yet well resolved, but fossil-calibrated studies suggest that they, along with flower-visiting Psittaciformes, diversified after the Eocene (Schweizer et al., 2011; Toon et al., 2010; Warren et al., 2003). These findings suggest that flower-visiting birds already existed 47 Ma ago and that plants acquired an ornithophilous flower morphology before the existence of their bird counterparts. Additionally, there is also evidence for cospeciation between birds and their floral resources. For instance, the oldest hummingbird clades, Hermits and Topazes, began diversifying around 18 and 25 million years ago (Abrahamczyk & Renner, 2015), respectively, which coincides with the diversification of the Heliconiaceae and Gesneriaceae families (Specht et al., 2012). Conversely, there are also examples in which plant diversification was facilitated by pre-existing hummingbird diversity (Abrahamczyk et al., 2017).

The shift from insect to bird pollination is suggested to have happened from a bee-pollinated ancestor (e.g. Zingiberales: Specht et al., 2012; Bromeliaceae: Kessler et al., 2020; hummingbird-pollinated plants: Barreto et al., 2024). According to Stephens et al. (2023), shifts from insect to vertebrate pollination have occurred multiple times in angiosperm history. Their results suggest that at least between 39-56 transitions have occurred in the whole angiosperm phylogeny. Three non-mutually exclusive mechanisms have been hypothesised to explain these shifts. First, birds' high mobility promotes high-distance pollen dispersal and therefore higher gene flow among plant populations (Cronk & Ojeda, 2008; Krauss et al., 2017, Dellinger et al., 2023). Nonetheless, Schmidt-Lebuhn et al. (2019) demonstrated how hummingbird-pollinated species from the genus *Justicia* (Acanthaceae) had shorter pollen dispersal distances. Second, the higher flower fidelity of birds under cold or wet conditions has also been proposed as an explanation for the shift (Cruden 1972). In this sense, shifts to vertebrate, or bird in particular, pollination seem to have coincided with mountain uplifts. Third, the lower pollen loss when plants use birds as their pollen dispersal vectors. Unlike bees that collect pollen to feed their offspring, birds generally do not consume pollen (Fleming & Moore, 2012). Likewise, birds do not groom pollen grains into pollen-carrying structures while foraging, therefore reducing its loss (Nicolson, 2007). Nonetheless, *Nectarina famosa* individuals have been observed removing orchid pollinia from their bills (Štěpán Janeček per. comm.). Yet, birds can transfer greater amounts of pollen as it was demonstrated in previous studies (Castellanos et al., 2003). Other evolutionary advantages of birds over insect pollinators relate to their longer life span, their great spatial memory, and their ability to revisit patchily distributed floral resources.

From an ecological perspective, the shift from bee to hummingbird (or bird in general) pollination can be explained by the occupation of new habitats and changes in the abundance or effectiveness of flowers or pollinators (Dellinger et al., 2021). In this sense, changes in certain environmental factors may reduce the frequency of the ancestral pollinator, resulting in pollen limitation (Thomson & Wilson, 2008). In this scenario, pollination by a second, previously less efficient, pollinator may then become more important. In the long run, this process may act as a selective pressure on the floral traits leading to reproductive isolation (Muchala, 2019). These processes may affect different parts of the flower in distinct ways, resulting in the formation of functional modules within the flower (Armbruster, 2014). Floral functional modules are integrated parts of the flower that can evolve independently of each other in response to pollinator-mediated selection (Opedal, 2019). This evolutionary independence is thought to facilitate shifts among pollinator functional groups in closely related plant species (Armbruster, 2014). Consequently, shifts in pollinator functional groups are only possible if changes in the frequency and effectiveness of pollinators are accompanied by changes in floral traits that accommodate the new pollinator group.

Pollination syndrome concept: Ornithophily vs Nectarivory

The diversity of floral morphologies has been largely attributed to the selection imposed by the diversity of pollinating agents. In addition, floral morphology is also the result of negative selection pressures exerted by floral antagonists. Yet, pollinator-mediated selection on floral traits has resulted in the convergence of floral morphologies, with pollination syndromes representing adaptations to specific functional pollinator groups (Fægri & van der Pijl, 1979). A pollinator functional group is therefore defined as pollinators that select for the same combination of floral traits (Fenster et al., 2004).

Traditionally nine syndromes have been recognised (Fægri & van der Pijl, 1979): Melittophily (bee), Ornithophily (bird), Chiropterophily (bat), Myophily (fly), Sphingophily (hawkmoths), Phalaenophily (most other months) Psychophily (butterfly), Cantharophily (beetle), and Sapromiophily (carrion and dung flies). Pollination syndromes are defined by floral traits that likely experience pollinator-mediated selection and reflect differences in the activity patterns, sensory capabilities, dietary and energetic needs, morphology, and behavior of pollinators (Muchala, 2007). Therefore, floral traits that normally are recorded include timing of floral anthesis, flower orientation, flower size and symmetry, corolla shape, the position of sexual organs, reward type, flower colour and scent (see Table 2 for a summary of each syndrome). The floral traits associated with a particular pollination syndrome ensure effective visitation by the corresponding functional pollinator group, thereby increasing the likelihood of successful reproduction.

Table 2. Summary of the traits that define the classical pollination syndromes as defined by Fægri & van der Pijl (1979). The table has been adapted from Wilmer (2011).

Syndrome	Functional group	Anthesis	Colour	Nectar guides	Scent	Shape	Nectar volume	Nectar concentration	Nectar site
Cantharophily	Beetles	Day / Night	Cream / Green	No	Strong / Fruity	Radial / Bowl shape	Low	Medium	Exposed
Myophily	Flies		White / Yellow	No	Mild / Not sweet	Radial / Flat	Low	Medium / High	Exposed
Sapromiophily	Carrion and dung flies	Day / Night	Purple / Red / Brown	No	Strong / Decaying	Radial / Bilateral	None	None	None
Psychophily	Butterflies	Day	Red /Orange / Yellow	Maybe	Mild / Sweet	Small / Long tube	Low	Low	Concealed
Phalaenophily	Moths	Dusk / Night	Cream / Yellow	No	Strong / Sweet	Radial / Short tube	Low / Medium	Low	Concealed
Sphingophily	Hawkmoths	Dusk / Night	White / Cream	No	Strong / Sweet	Radial / Long tube / Spur	Medium	Medium	Concealed
Melittophily	Bees	Dawn / Day	Pink / Purple / Blue	Yes	Mild / Sweet	Bilateral / Radial / Short tube	Medium	Medium	Exposed / Concealed
Ornithophily	Birds	Day	Red / Orange	No	None	Bilateral / Radial / Medium tube	High	Low	Concealed
Chiropterophily	Bats	Dusk / Night	Dull white / Dull beige	No	Strong / Fruity	Bilateral / Radial / Bowl / Brush	High	Medium	Exposed

Ornithophilous flowers are normally characterized by having a red colour, long and narrow corolla tubes, producing high volumes of rather diluted nectar, and absence of scent (Cronk & Ojeda, 2008). Additional traits involve the positioning and protection of the flowers, with hummingbird-pollinated flowers typically being pendant and mechanically reinforced to withstand large-bodied birds. **Could these traits have evolved for reasons other than attracting birds?** For example, the red colouration has been suggested to deter bees rather than to attract birds (Proctor et al., 1996). As opposed to birds, which perceive wavelengths between 300 and 660 nm, bees cannot see the red colour (i.e., bee vision spectrum: 300-550 nm). In this context, neotropical ornithophilous flowers exhibit a median wavelength of 585 nm, which lies outside the visual range of bees (Altshuler, 2003). As mentioned above ornithophilous flowers produce large volumes of rather diluted nectar. Nectar volume is generally correlated with flower size (Baker, 1978), but at equal sizes, bird-pollinated plants produce larger amounts than bee-pollinated ones. Sugar concentrations in bird-pollinated flowers range between 20% and 26% (Proctor et al., 1996). The concentration determines the viscosity of the nectar and therefore the ease with which birds uptake the nectar (Köhler et al., 2010). Moreover, dilute nectar, like that of ornithophilous plants, is not optimal for bee pollinators therefore making it a deterrence mechanism (Bolten & Feinsinger, 1978). Finally, another important aspect is nectar sugar composition. For example, flowers pollinated by specialised birds have high contents of sucrose in the nectar, whereas that of plants visited by generalised birds is rich in hexoses (Johnson & Nicolson, 2008). Moreover, other studies have demonstrated that the nectar of passerine-pollinated plant species aligns with that of hummingbird-pollinated plant species (Bartoš et al., 2012; Janeček et al., 2021).

As a result of coevolution with flower morphology, nectarivorous birds tend to have long bills with varying degrees of curvature (Feinsinger & Colwell, 1978). An extreme case are the Neotropical sicklebill hummingbirds (*Eutoxeres spp.*). Another adaptation to nectarivory is the small body size of nectarivorous birds (Brown et al., 1978). Yet, this comes at a cost, as the small size increases the energetic expenditure due to poorer thermoregulatory capabilities. This situation is overcome by the abundant energy supplied by nectar. Due to the unique nature of their diet, nectarivorous birds must have a highly efficient liquid extraction mechanism. At first, it was believed that nectar uptake happened by capillarity. Instead, Rico-Guevara & Rubega (2011) demonstrated that hummingbirds' tongues dynamically trap nectar by quickly changing their morphology. These authors propose that this mechanism should be present in other nectarivorous birds due to the convergent nature of their tongues. Other adaptations related to the consumption of nectar involve changes in the gastrointestinal tract of the birds. For example, nectarivorous birds have shorter intestines due to the highly digestible nature of nectar (Richardson & Wooller, 1986). Moreover, nectar is hypertonic relative to the avian plasma, and therefore the bird's intestine has a mechanism to avoid dehydration by passive uptake of glucose (Del Rio & Karasov, 1990).

The pollination syndrome concept has been widely applied to predict the visitation of pollinators to a plant species (e.g., Danieli-Silva et al., 2012; Lagomarsino et al., 2017; Martén-Rodríguez et al., 2009; Paw, 2006). Despite its apparent utility, the pollination syndrome is not without controversy. One of the main criticisms against the usefulness of pollination syndromes is that they are oversimplified given that most plant species are visited by more than one functional group (Waser et al., 1996). Nonetheless, the fundamental assumption of the pollination-syndrome concept is that flowers co-adapt with their most frequent and effective pollinator functional group (Ashworth et al., 2015; Stebbins, 1970). In favor of these ideas, Rosas-Guerrero et al. (2014) found support for the pollination syndrome concept demonstrating that floral trait convergence is driven by the most effective pollinator. On the other hand, Ollerton et al. (2009) found little support for the pollination syndrome predicting only c. 30 % of all pollinators. Moreover, these authors found that the realised trait combinations in actual flowers do not match the traditional syndromes. Another issue is that pollination syndromes are defined by different trait combinations in different parts of the world. For example, the chiropterophily in the Old and the New World tropics is characterised by different trait combinations (Fleming et al., 2009). Similarly, Ornithophilous flowers in the Old World generally have a perch from where the bird forages, whereas their New World counterparts usually lack this feature (Cronk & Ojeda, 2008).

Instead of rejecting or accepting the legitimacy of the pollination syndrome concept, few considerations should be taken into account. First, not all the traits are equally important in predicting the interactions (Dellinger, 2020). For example, in **Chapter IV**, we demonstrated how nectar reward is the most important trait in explaining sunbird-plant interactions. Second, the inclusion of new traits might help to better predict the visitor to a particular plant species. In recent years, quantitative analyses of floral scent through gas chromatography techniques have helped to refine the pollination syndrome (Schiestl & Dötterl, 2012). Third, pollination studies should try to focus on community-wide studies, rather than specialised pollination systems. In this context, more research effort should be put into generalised pollination systems (Vasconcelos et al., 2019), as they can bring new insights into the coevolution between plants and their pollinators. Finally, researchers should try to quantify the relative importance of the different functional pollinator groups, instead of just documenting their visitation (Santiago-Hernández et al., 2019). In this sense, some studies have provided evidence that just a subset of all visitors acted as effective pollinators (Bartoš et al., 2015; Janeček et al., 2007).

Drivers of bird-plant pollination interactions

Despite years of pollination research, the drivers of plant-pollinator interactions are still a matter of debate. Two main processes have been proposed as the determinants of the structural patterns of plant-pollinator networks (Vázquez et al., 2009a). Research has shown that the interactions can be explained by *neutral processes*, where the abundance of each interacting species plays a major role (Dupont et al., 2003; Ollerton, 2003). Consequently, network architecture is the result of the random encounters of each interacting partner, regardless of their traits. In this context, the interaction strength of abundant species is higher than that of rare ones. Evidence for abundance predicting species interactions comes from plant-insect interaction networks (Sazatornil et al., 2016; Vázquez et al., 2009b), but also from bird-plant interaction networks (**Chapter I**; Uceda-Gómez et al., 2024). On the contrary, plant-pollinator interactions can be mediated by the traits of the interacting partners (Stang et al., 2007). Therefore, *niche-based processes* govern the observed interactions among plants and pollinators, with two hypotheses proposed.

First, the *"forbidden links hypothesis"* postulates that the intrinsic biological characteristics of a species determine whether an interaction occurs. Several mechanisms can result in forbidden links, for example, spatiotemporal non-overlap in species distribution or activity (Jordano et al., 2006), or exploitation barriers (Santamaría & Rodríguez-Gironés, 2007; Snow & Snow, 1972). For example, plant-hummingbird networks were defined by the spatiotemporal mismatch of the interacting partners, as well as the definition of interaction modules due to bill-corolla length matching (Maruyama et al., 2014). Moreover, bird-plant networks (i.e., visitation and pollination) were best explained by phenology in the Andean elfin forest of Peru (Gonzalez & Loiselle, 2016).

Second, bird-plant interactions, or pollination interactions in general, can be the result of *morphological trait-matching*. This hypothesis predicts that among all the potential interactions, pollinators would visit more frequently those plants whose flower morphology matches with their mouthparts. Therefore, trait-matching is the result of specialization, achieved either through reciprocal co-evolutionary processes, one-sided evolutionary processes to accommodate new pollinators, or via ecological fitting between species with independent evolutionary trajectories (Guimarães et al., 2011; Janeček et al., 2020; Janzen, 1980; Whittall & Hodges, 2007). In support of this hypothesis, Maglianesi et al., (2014) found that the association of bill and corolla length enabled hummingbirds to extract the floral resources more efficiently. Furthermore, Janeček et al. (2012) showed that the long-billed *Cyanomitra oritis* visited plants with the longest floral tubes. Moreover, Sonne et al. (2019) demonstrated how trait-matching structures hummingbird-plant interactions in the eastern high Andes. In their study, these authors also showed how trait matching also presents a geographical distribution. The longest corollas were found at high elevations, where hummingbirds with the longest bills occur. These results also align with those of Hořák & Janeček (2021), which demonstrated that sunbird bill length and *Impatiens spp*. spur length match across several geographical regions.

It is important to note that all three hypothetical mechanisms (i.e. neutral processes, forbidden links, morphological trait-matching) mentioned above are not mutually exclusive and all can govern the structuring of any pollination network, yet their actual contribution is still a matter of discussion (Vázquez et al., 2009b). Vizentin-Bugoni et al. (2018) pleaded for the existence of a *continuum* of importance from niche-based processes to neutrality in shaping plant-pollinator interactions. These authors developed a simple conceptual model in which the importance of each process depends on the extent of trait variation within the assemblage. In a scenario where plants and pollinators show a lot of trait variation niche-based processes will prevail, whereas the opposite is expected when trait variation is less pronounced (i.e., low vs high functional diversity). Finally, since seasonality can influence plant phenological patterns in the tropics, trait variation is subject to these changes. For instance, Klomberg et al. (2022) observed a higher prevalence of ornithophilous flowers during the rainy season on Mount Cameroon, which may ultimately impact the significance of niche-based processes.

Spatiotemporal variability in bird-plant pollination interactions

The application of network theory to the study of plant-pollinator interactions has provided valuable insights into the structural characteristics of these networks and their role in ecosystem functioning (Blüthgen et al., 2006). Specialization emerges as a key aspect of ecosystems, and therefore understanding how different environmental conditions affect it is fundamental. This knowledge can help to shed light on the potential impacts of climate change on plant-pollinator interactions (Hoiss et al., 2015), as well as offer insights into evolutionary and speciation processes (Ramírez et al., 2011).

Specialization is a double-faceted concept, and two levels must be distinguished (Blüthgen et al., 2006). When interactions are contemplated as ecological niches, the first level describes the niche breadth of a species, whereas the second represents the extent to which several species partition their niches. These two concepts are mainly shaped by the tendency of plants and pollinators to use a subset of all available resources, or by interspecific mechanisms such as competition. In plant-pollinator interactions, specialist species are those that interact with a limited number of plant species (Armbruster et al., 2000). The extent to which plant-pollinator networks are specialised influences the structure of the network, with low specialization promoting network stability (Blüthgen & Klein, 2011). Therefore, generalised networks are thus more resistant to species loss. On the other hand, high levels of pollinator specialization can be important for plant reproduction. In this sense, specialization decreases the deposition of heterospecific pollen, promoting plant reproduction.

Specialization can result from several ecological and evolutionary processes that function at different spatial and temporal scales (Carnicer et al., 2009). For example, it might be the outcome of niche-based processes (i.e. forbidden links or trait-matching) by constraining the type, number and strength of interactions of a species in the network (Stang et al., 2007). Additionally, specialization can result from spatiotemporal variation in resource availability (González-Castro et al., 2012). Therefore, elevational gradients with their steep abiotic changes over a short geographic distance, offer a unique opportunity to investigate how specialization varies with elevation.

For example, Maglianesi et al. (2015) found that hummingbird species and individuals were more specialised in the low and middle elevations. These authors used the d' index to measure specialization, which determines resource use by a pollinator based on the abundance of resources (Blüthgen et al., 2006). The specialization pattern observed was linked to a more even and functionally overdispersed assemblage at the lower elevations, indicating a significant level of floral resource partitioning. Conversely, the highland community displayed a clustered functional structure, likely due to environmental filtering and niche expansion. Moreover, Maglianesi et al. (2014) found that hummingbird-plant networks were more specialised at middle elevations, measured as the H'_2 index. This index measures specialization at the network level and thus considers both plants and pollinators. Therefore, H'_2 is a measure of niche partitioning (Blüthgen et al., 2006). On the contrary, Partida-Lara et al. (2018) found that hummingbird-plant networks were more specialised at high elevations. Likewise, Pellissier et al. (2018) found that connectance lowered at high elevations. Connectance is the proportion of realised links relative to all possible interactions. Thus, a decrease in connectance translates into higher specialization.

The composition of the different flower-visiting functional group communities also varies along elevational gradients (Maguiña-Conde et al., 2023). In this sense, elevational gradients affect the diversity and frequency of visiting functional pollinator groups. Plants with broad elevational distributions must locally adapt to the pollinator community, because of the filtering effects of elevation on different pollinator functional groups. Therefore, visitors of a single plant species can differ among individual populations or phenological periods (Thompson, 2005). In this scenario, a geographical coevolutionary mosaic between plants and their floral visitors is expected (Anderson & Johnson, 2007). Thus, differences in the diversity and frequency of different pollinator functional groups can trigger covariation processes among pollinator and floral traits. For example, Cuartas-Hernández et al. (2019) showed how two sympatric *Anthurium* spp. species covaried in their floral traits with their main floral visitors along an elevational gradient in the Colombian Andes. Likewise, Maguiña-Conde et al. (2023) found a strong correlation between pollinator and floral traits of *Costus guanaiensis* along a neotropical elevational gradient.

Pollinator functional group turnover along an elevational gradient is often mediated by changes in abiotic conditions (e.g., temperature or rainfall). For example, McCabe & Cobb, (2021) observed a bee-to-fly transition because of decreasing temperatures. Several studies across the globe have found support for this transition (Kuriya et al., 2015; Lay et al., 2013; Nagano et al., 2014; Sommaggio et al., 2022). Therefore, there is a zonation of different pollinator functional groups across elevational gradients due to the physiological constraints of pollinators in coping with harsh mountaintop conditions (Adedoja et al., 2018; Lefebvre et al., 2018).

On the other hand, birds, as endothermic animals, can fly in more windy and rainy conditions, and consequently, are less affected by unfavourable weather conditions on mountain tops (Dellinger et al., 2021). Therefore, birds are better pollinators at high-altitude ecosystems. For example, ornithophilous plants were more effectively pollinated than closely related bee-pollinated species at high elevations in Mexico (Cruden, 1972). Similarly, Lehmann et al. (2019) observed a shift in pollinator functional groups, with hummingbirds serving as the primary pollinators of *Gonzalagunia hirsuta* at high elevations on Dominica island. Evidence for birds being more effective pollinators at high elevations also comes from the Old World. Pollinator exclusion experiments demonstrated that several *Rhododendrom* species heavily depend on sunbirds at high elevations in the Yunnan Province in southwest China (Huang et al., 2017). Equally, Pi et al. (2021) found that *Eleagnus umbellata* populations at high elevations relied more heavily on sunbirds for pollination services.

In addition to the effects of spatial variability (e.g., elevation) on bird-plant interaction networks, we should also consider their temporal variability. Temporal changes in the availability of resources can affect the way plants and birds interact. Partida-Lara et al. (2018) demonstrated how humming-plant networks were more specialised when resource availability was low. These results are supported by indirect evidence showing that the amount of nectar and the diversity of interacting partners available for various bird taxa can vary significantly from season to season (e.g., for hummingbirds: Abrahamczyk & Kessler, 2010; for sunbirds: Collins & Rebelo, 1987). Moreover, Maruyama et al. (2014) demonstrated that phenological overlap between the plants and hummingbirds influences the establishment of network modules, where certain sets of species interact more frequently with other than with other species. Yet, temporal variability not only affects network structural features but also can favour the presence of certain pollinator functional groups. Klomberg et al. (2022) and Janeček et al. (2015) found higher numbers of ornithophilous plants during the rainy season of Mount Cameroon. These findings indirectly suggest that bird pollination is favoured under rainy conditions, aligning with the results presented in **Chapters I** and **VI** of this thesis. We demonstrate that trait-matching and the specialization of sunbird-plant networks, as well as individual sunbird species, increase during the rainy season.

Study sites

As stated before, the pollination syndrome concept assumes that most interactions are highly specialised. Nevertheless, more recent studies suggest that specialized interactions are rather rare and that pollination systems are more generalised than previously thought (Waser, 1996). Present, community-wide studies have demonstrated that generalised pollinators are the most important actors for plant biodiversity maintenance. Moreover, they have demonstrated that plants and pollinators interact with one another in an asymmetric fashion (i.e. specialists interact with generalists), which strengthens the robustness of the ecosystem. As a result, pollination networks tend to be highly nested and modular, as in the network terminology.

Similar patterns as described above can be found for bird-plant pollination networks. Nonetheless, most of our knowledge about bird pollination comes from the New World hummingbirds. Pollination facilitated by avian species is documented or anticipated across over 70 distinct bird families (Ollerton, 2024). Notably, among these families, three exhibit pronounced specialization towards nectarivory: Hummingbirds (Trochillidae), sunbirds (Nectariniidae), and honeyeaters (Meliphagidae). Hummingbirds (Apodiformes) with 363 described species are the most species-rich taxon, having a Pan-American distribution. On the other hand, sunbirds (Passeriformes, 143 species) are distributed across Africa, Asia, and Oceania, while honeyeaters' distribution extends from Asia to Oceania. These three taxa share common adaptations for nectarivory and showcase an example of convergent evolution. This convergent evolution has raised a great deal of interest among the scientific community, which has tried to understand the differences in morphology and ecology among the three taxa (e.g.

Zanata et al., 2017). It is widely accepted that hummingbirds are the most specialised family for bird pollination. Nonetheless, studies on the other two families are rather scarce.

Another important aspect of pollination research is to shed light on the processes that shape the observed interactions. In this regard, most of the pollination studies have focused on factors related to the diversity of the interacting partners, their abundances, and phylogenetic relationships, as well as their morphological traits. However, changes in the interaction networks due to spatiotemporal variation have received less attention.

Pollination research in Africa has primarily concentrated on subtropical and temperate regions, although there are some notable exceptions. For example, Classen et al. (2020) studied the effects of elevation on the specialization of pollinator-plant interactions along a 3.4 Km elevational gradient on Mount Kilimanjaro. Moreover, Mertens et al. (2020) studied the turnover of floral visitors on *Scadoxus cinnabarinus* along its elevational gradient on Mount Cameroon. Further, Padyšáková et al., (2013) investigated the roles of floral visitors on *Hypoestes aristata*. Studies focusing on bird pollination also exist. For example, Bartoš & Janeček (2014) studied the pollen placement mechanism of *Impatiens frithii* on the sunbird's body, reducing interspecific competition among congeners. Moreover, Bartoš et al. (2012) investigated the nectar properties of *Impatiens sakeriana,* while Janeček et al., (2012) studied the pollination systems of several flowering plants, both studies conducted on Mount Cameroon. Finally, Nsor et al., (2019) conducted a study on sunbird-plant pollination networks. They reconstructed a sunbird-plant pollen transfer and visitation network on the Mambilla Plateau in southeast Nigeria. Nonetheless, these authors only sampled sunbird-plant interaction networks during the dry season, neglecting the effects of temporal variation on the interaction networks.

We set out to Mount Cameroon (4.203°N, 9.170°E) to gain insights into bird-plant interactions and how spatiotemporal variability affects them. Mount Cameroon is in the Southwest Region of Cameroon and is the highest mountain in West-Central Africa. Moreover, Mt. Cameroon is an active volcano belonging to a greater volcanic mountain range that stretches from the island of Bioko (Equatorial Guinea) and across Bamenda Highlands following the Nigerian border. Due to its unique location next to the Gulf of Guinea and its proximity to the Guinean and Congolese biotopes it presents high levels of diversity and endemism. For example, the Mount Cameroon speirops (Zosteropidae; *Zosterops melanocephalus*) a generalist flower visitor is endemic to Mt. Cameroon. Mount Cameroon still has an almost pristine continuous forest elevational gradient (~ 400 to ~2200 m. a.s.l.) on its southwestern slope. It was along this gradient that we sampled sunbird-plant interactions at four locations encompassing four forest types (Table 3 and Fig. 4). The dataset collected in this gradient was used in **Chapters I**, **III**, **IV**, and **VI**. Moreover, we extended our sampling above the timberline to the montane grasslands, where we focused on sunbird-plant interaction networks, and the effects of elevation on the turnover of floral visitors on the main food resource at these elevations (i.e., *Hypericum revolutum;* Hypericaceae). The dataset from the montane grasslands was used in **Chapters V** & **VII**. Additionally, in **Chapter II**, we sampled sunbird-plant interactions in the farmlands on the foothills of Mount Cameroon, where local farmers grow exotic plants for exportation and sale in local markets.

Mount Cameroon experiences distinct seasonality (Maicher et al., 2020), with a dry period from mid-November to February and a wet season with heavy rains from June to September. Precipitation in the forest elevational gradient can reach up to 2500 mm in the two lowest elevations. Temperatures are constant along the year, ranging from c. 25 °C in the lowest elevation down to 15 °C at 2200 m a.s.l. These two seasons are intertwined with two interseasons. **Chapters I** and **III-VI** were conducted in both dry and wet seasons, whereas

Chapter VII was conducted in the two interseason periods. The sampling of **Chapter II** stretched from the interseason from dry to wet season to the wet season.

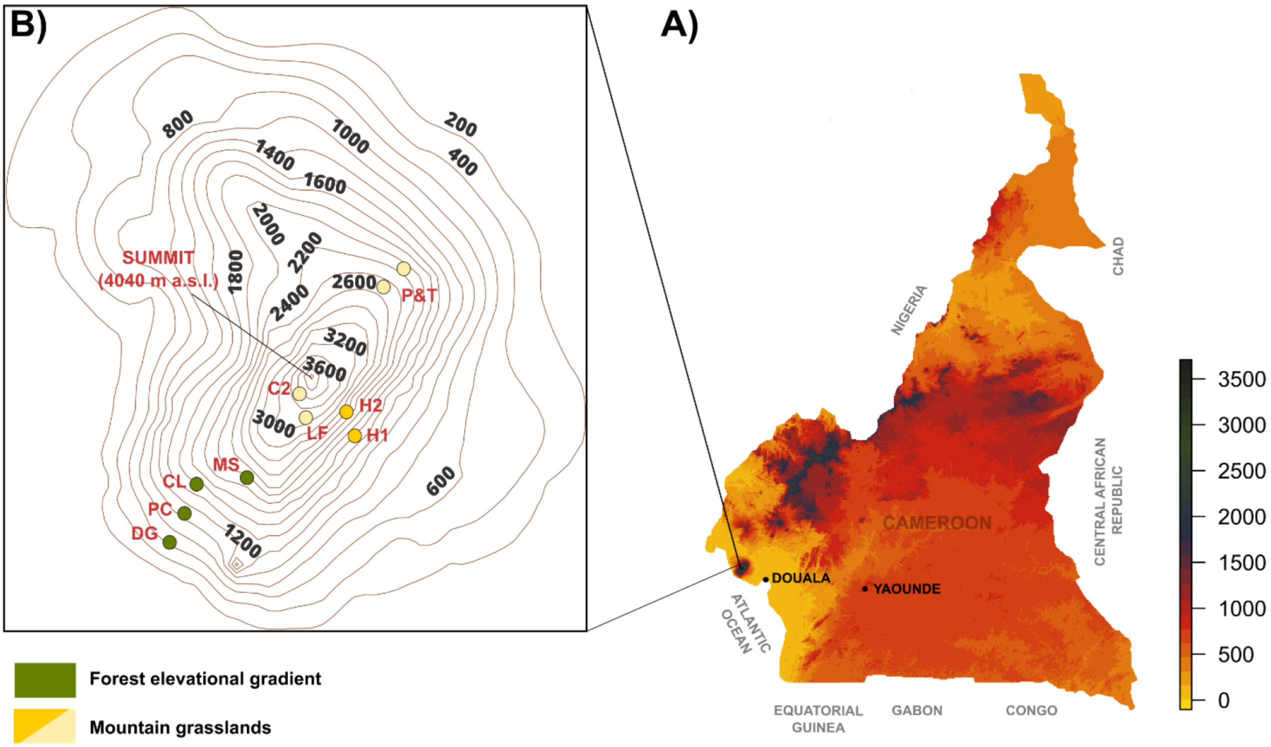

Figure 4. Location of Mount Cameroon and the sampling points within Cameroon used in this thesis: **A)** Topographical map of Cameroon; **B)** Topographical map of Mount Cameroon with the geographical position of our sampling locations. In green, locations in the forest elevational gradient (**Chapters I, III, IV,** and **VI**): Drinking Garri (DG), PlanteCam (PC), Crater Lake (CL), and Mann's Spring (MS). In yellow, locations in the montane grasslands. Note the two shades of yellow representing two different projects conduced in this habitat type (dark yellow, **Chapter V**; light yellow, **Chapter VII**).

Table 3. Detail of the sampling localities and their year of sampling. Each sampling site was sampled two times. The colours depict the two different habitat types sampled: forest elevational gradient (in green), and montane grasslands (in yellow).

Site	Coordinates	Elevation (m a.s.l.)	Description	Sampling year
Drink Garri	N 04.1022°, E 09.1225°	650	Lowland forest, minimally disturbed by elephants, where trees of the subfamily Caesalpinioideae (Family: *Fabaceae*) prevail.	2018-2019
PlanteCam	N 4.1175°, E 09.0717°	1100	Mid-elevation forest, partly disturbed by elephants, where *Kigelia africana*, *Macaranga occidentalis* and *Voacanga africana* are common.	2018-2019
Crater Lake	N 04.1443°, E 09.0709°	1500	Submontane forest, highly disturbed by elephants, where open elephant pastures are common and where *Aframomum* spp. prevails.	2019-2020
Mann's Spring	N 04.1428°, E 09.0630°	2200	Montane forest, close to the timberline, where elephant disturbance is absent and where montane species like *Syzigium staudtii*, *Nuxia congesta* and *Schefflera* spp. are common	2019-2020
Hut 1	N 04.1759 °, E 09.2041 °	2100	Species-poor low-elevational communities relatively dominated by tall grasses, *Cenchrus monostigma*, and *Loudetia simplex*. There are not many species specific to these grasslands e.g. *Habenaria mannii*. In these communities, we can also find herbs (e.g. *Lobelia columnaris*) or scattered trees (e.g. *Nuxia congesta*).	2021-2022
Hut 2	N 04.1938 °, E 09.1938 °	2800	High-elevation grasslands are species-rich grasslands with a common occurrence of grasses, such as *Andropogon spp.*, *Sporobolus montanus*, and *Koeleria capensis*. Taller vegetation with *Pentas schimperiana* or *Hypericum revolutum* can be found locally in leeward areas.	2021-2022
P&T-1	N 04.3068 °, E 09.2297	2300	Species-poor low-elevational montane grasslands dominated by the tall grass *Laudetia symplex*.	2021-2022
P&T-2	N 04.2715 °, E 09.2206 °	2800	Mid-elevation montane grasslands representing the transition from high to short grasslands.	2021-2022
'89 Lava low	N 04.1911 °, E 09.1776 °	3200	Species rich grasslands with typical occurrence of *Andropogon spp., Sporobolus montanus,* and *Koeleria capensis*.	2021-2022
Camp-2	N 04.2103 °, E 09.5972 °	3500	Sparse vegetation dominated by *Festuca abyssinica*.	2021-2022

2. OUTLINE OF THE DISSERTATION

Aims

In this dissertation, the main goal was to provide insights into the bird pollination systems from a relatively understudied region of the world and contribute to the understanding of the ecology of sunbirds (Nectariniidae). In doing so, we have furthered our understanding of the bird pollination syndrome concept as a way to predict the observed interactions. We have also challenged hypotheses related to the segregation of bird-feeding niches according to the complex of visited plant traits, as well as the level of trait-matching between the interacting partners. Pollination syndromes are one of the central concepts of plant adaptation, where plants pollinated by the same pollinator group are hypothesised to share similar floral traits via convergent evolution (Faegri and van der Pijl 1979, Fenster et al. 2004, Rosas-Guerrero et al. 2014). Thus, the pollination syndrome concept was proposed as a predictive framework to predict all the potential visitors that a plant could receive. Moreover, the pollination syndrome theory relies on the tight coevolution between the interacting partners, like a Darwinian coevolutionary arms race. Nonetheless, in recent decades, community-wide studies have demonstrated that these tight relationships are rather exceptional in nature. In this sense, nectarivorous birds have been observed visiting non-ornithophilous plants, and insects have been observed visiting ornithophilous ones (Chmel et al., 2021).

Additionally, we aimed to investigate the spatiotemporal variability of bird-plant interactions. Elevational gradients offer unique field laboratories marked by swift environmental transitions, ideal for testing hypotheses regarding the impact of abiotic factors on the interaction networks. Moreover, seasonality may affect the availability of resources for bird pollinators, ultimately affecting the structure of the observed networks. Thus, we aimed to test how specialised/generalised our networks are, aligning with the predictions of the altitudinal niche-breadth hypothesis in plant-pollinator interactions (Rasmann et al., 2014). Finally, we also aimed to test the effect of elevation on the differential distribution of different pollinator functional groups, with a special focus on bird visitors.

To sum up, this dissertation mainly aims to:

a. Gain a better understanding of the processes shaping sunbird-plant interactions, as well as challenging the concept of bird pollination syndrome (**Chapters I-IV**)
b. Shedding light on whether sunbird species segregate their feeding niches according to the traits of the visited plants, and their correspondence with bird traits (**Chapters I, III, & V**).
c. Identifying the effects of spatiotemporal variability on sunbird-plant networks (**Chapters I, V, VI & VII**).

Outline and outcomes

Chapter I focused on the different drivers that could explain the observed interactions and their respective seasonal variations. As explained in the introduction, still there is much debate among the scientific community and the conclusions vary from study to study. Our study aimed to explore whether sunbird-plant interactions are explained by neutral and/or niche-based processes, as well as to determine whether there is seasonal variation in their importance. Moreover, we investigated the roles of trait-matching and the effects of robbing on the observed interactions. To achieve this goal, we employed a diverse array of statistical techniques, encompassing null modelling, multivariate statistics, and probabilistic modelling. Within the realm of probabilistic modelling, we accounted for various factors: the abundance of interacting partners as a proxy for neutral processes, morphology representing niche-based processes, and nectar sugar content reflecting the quantity of offered rewards. Our results indicate that sunbird-plant interactions can be explained by both processes considered. In this sense, during the dry season, neutral processes drive bird visitation, whereas the importance of niche-based processes increases during the wet season. Moreover, of all bird traits tested (i.e. bill length, bill width, bill height, and weight), only the bill length was able to predict the complex of visited plant traits, when robbing events were excluded. Another outcome of this study was the overlap of sunbird feeding niches when all species were considered together. Although this question remains to be tested, we hypothesise that this pattern of niche overlap is probably due to the absence of competition among sunbirds. In this context, we observed that in both seasons, certain plants acted as hubs attracting most of bird visitors. Nonetheless, during the wet season, the blossoming of ornithophilous plants might explain the increased importance of trait-based processes in this period.

Due to this temporal variation in the importance of these two processes, I propose that the sunbird-plant interactions could be interpreted as a continuum between visiting the most abundant plants and those that produce suitable amounts of sucrose-rich nectar, like what was suggested by Vizentin-Bugoni et al. (2018). In this context, the relationship between bill and corolla tube length will serve as a filter enabling certain legitimate interactions.

Chapter II investigated if local bird communities, with different evolutionary trajectories, were able to pollinate alien plant species. Understanding the answer to this question holds significance in unravelling the implications of convergent evolution processes. We performed an experiment at a farm situated in the foothills of Mount Cameroon, where local plant producers cultivate ornamental plants belonging to the genera *Etlingera* and *Heliconia*. *Etlingera* is a genus pollinated by spiderhunters (Nectariniidae; Arachnothera) from Asia, whereas *Heliconia* is a neotropical genus pollinated by hummingbirds (Trochilidae). In this setup we aimed to test the following scenarios: (a) Total incompatibility, local sunbirds do not visit any of the plants that evolved on different continents; (b) Partial ecological fitting, when birds visit the plants but do not pollinate them; (c) Complete ecological fitting, when birds visit alien plants and successfully pollinate them. Our research revealed strong ecological compatibility between actors with diverse evolutionary backgrounds, affirming the broad applicability of the bird-pollination syndrome. Additionally, we highlight the significance of trait-matching and niche differentiation as essential ecological mechanisms, even within semi-artificial environments. Our findings complement Janzen's (1985) notion that many observed interactions result from ecological fitting rather than strict coevolutionary processes within a specific locale. Nonetheless, *Etlingera spp.* had tighter interactions with local sunbird assemblages, possibly due to the shared evolutionary history with their natural pollinators.

In **Chapter III**, we experimentally tested the sunbirds' preference for ornithophilous plants. Specifically, we investigated the preference for *Impatiens sakeriana* among two sunbird species: *Cinnyris reichenowi* and *Cyanomitra oritis*. We established experimental setups at two distinct elevations: the mountain forest and the mid-elevational forest on Mount Cameroon. In a cage experiment, we presented four plant species to the birds from the two different altitudinal forest types. These species included two mountain species, *Impatiens sakeriana* and *Nuxia congesta*, and two mid-elevational forest species, *Tabernaemontana ventricosa* and *Kigelia africana*. Among these species, only *I. sakeriana* exhibits bird pollination syndrome. Additionally, to test whether we found different visitation patterns on the target plant species among the two sunbird species, we performed observation of bird visitation under natural conditions. We hypothesised that target sunbird species segregate their feeding niches and differentiate in their rate of visitation to the target plant species under natural conditions. Second, this niche segregation is reflected under natural conditions. Moreover, we expected sunbird individuals to prefer those plant species growing in the elevation where the experiment was being conducted. Lastly, we expected sunbirds to show an innate preference for ornithophilous plants (i.e. *I. sakeriana*).

Our results demonstrated that there was niche segregation among the two sunbird species with respect to our focal plants. The segregation was manifested in the relative visitation ratios to short and long-tubed plant species, aligning with the morphological characteristics of the bird visitors. In this sense, these results agree with those of **Chapter I** and emphasize the importance of the relationship between bill and tube length. The preferences exhibited by the birds under experimental conditions closely mirrored their feeding patterns observed in natural settings. During the cage experiment, sunbirds were observed to occasionally visit all plant species, regardless of their pollination syndromes or whether they were native or introduced. Interestingly, the most preferred plant species was *T. ventricosa*, despite it having a moth pollination syndrome. Regardless of its ornithophily, *I. sakeriana* was not preferred for mid-elevational forest birds. Nonetheless, mountain forest birds preferred *I. sakeriana* over *N. congesta*, probably because of associative learning mediated by higher nectar rewards.

The validity of the bird pollination syndrome for birds on Mount Cameroon was tested in **Chapter IV**. Additionally, we tested whether floral traits were able to predict the visited plant species, or if sunbird visitation was driven by offered nectar reward. We combined a dataset of insect-plant interactions with our sunbird-plant interaction dataset (used in **Chapters I & VI**) from the same sampling locations on Mount Cameroon. To do so we used a simple conceptual model aiming to answer: (a) whether both functional groups visit different groups of plants; (b) if ornithophilous plants interacted mainly with sunbirds; (c) if sunbirds interacted more frequently with plants bearing ornithophilous traits, and (d) if the complex of floral traits was able to predict bird visitation. We found a continuum of strategies in which birds and insects visited plants bearing both types of pollination syndromes. Nonetheless, from the plant's point of view, we confirmed the validity of the bird pollination syndrome. Ornithophilous plants were visited at a higher rate by sunbirds. On the other hand, nectar production was the best predictor of sunbird visitation. Sunbirds visited plants bearing other pollination syndromes (e.g. *Anthonotha fragans* or *Nuxia congesta*), which entailed a huge amount of nectar, especially during the dry season.

Chapter V serves as a hinge among the two main topics that structure this thesis, namely niche segregation in relation to the bird pollination syndrome, and sunbird-plant interactions along environmental gradients (i.e., elevation and seasonality). In this study, we aimed to study sexual niche segregation because of nectar competition. As model species we used the sexually dimorphic Volcano Sunbird (*Cinnyris preussi;* Fig. 5). We studied the sunbird-plant interactions along an elevational gradient stretching from 1100 to 2800 m a.s.l. and in two contrasting seasons.

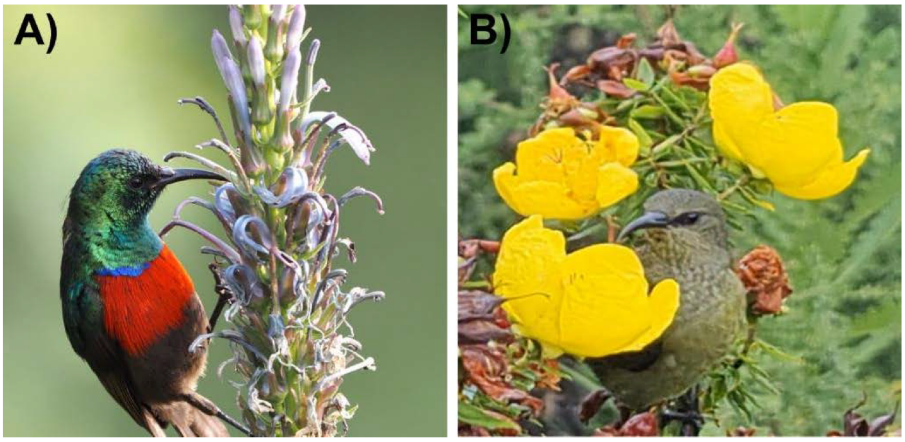

Figure 5. A) Male of Vulcano sunbird on *Lobelia columnaris*; **B)** Female of the same species on *Hypericum revolutum* (® Štěpán Janeček).

Our study sought to examine potential differences in feeding behavior between male and female birds, focusing on their preference for particular plant species. Additionally, we investigated whether females with shorter bills exhibit a preference for short-tubed plants and whether larger dominant males show a preference for flowers with higher nectar production. We also explored the spatial segregation of feeding niches along an elevation gradient and assessed whether this segregation varied between contrasting seasons. Despite the extensive dataset comprising 6476 interactions between birds and plants, our analysis revealed no significant disparities in the spectrum of visited plant species. Contrary to our initial hypotheses, females did not exhibit a preference for flowers with shorter tubes, nor did males show a predilection for flowers with higher nectar yields. However, an intriguing observation emerged during the wet season, wherein we noted a sex-specific dispersion pattern among sunbirds. The predominant factor influencing sunbird behavior appears to be the abundance of nectar-rich, generalized plants frequently visited by these birds, aligning with the results of **Chapters I** and **IV**. This pattern is particularly evident during the dry season when there is a high overlap in observed niches. In the montane forest, these trees either lack floral tubes (e.g., *Astropanax abyssinicum*, *Syzigium spp*.) or possess relatively short tubes (e.g., *N. congesta*), allowing easy access to nectar for both male and female sunbirds. *T. ventricosa*, occurring in the submontane forest, has slightly longer floral tubes, it is adapted to moth pollination and does not align with sunbirds' beak morphology. In montane grasslands, *Hypericum revolutum*, a bee-pollinated plant with flat, morphologically generalized flowers, stands out as one of the most visited plants in both dry and wet seasons. Thus, niche overlap is obscured due to the high asymmetrical relationship between sunbirds and plants. One exciting result was that during the wet season, there was a significant decrease in nectar production within these habitats, leading to a considerable decline in female presence. Conversely, female activity notably intensified at both the lowest and highest extremes of the altitudinal range.

In the next two chapters, we explored more in depth the effects of altitude and temporal variability in sunbird-plant networks. In this sense, **Chapter VI** addressed the question of how elevation and seasonality affected the structural features of the sunbird-plant networks. Similar studies addressed these questions; however, they were constrained to environments at high elevations and during the dry season. Our aim was to study the level of specialization or generalization of sunbird-plant networks in relation to both environmental gradients (i.e., elevation and seasonality). Our results indicate that sunbirds living at high elevations, as well as the entire networks, were highly generalized. Nonetheless, low-elevation sunbird-plant communities were much more specialised. Moreover, the wet season showed higher levels of specialization. As in **Chapters I, IV, and V** these results are probably due to the phenological patterns of ornithophilous plants, which blossom predominantly during the wet season. With **Chapter VII** we move outside the forest elevational gradient, to explore the relationship between bird visitation and elevation. As elevation rises, a shift in pollinator functional groups is anticipated, driven by altitude. Previous research has shown that birds tend to function better as pollinators at higher altitudes compared to bees. Furthermore, an elevation-driven transition from bees to flies with increasing elevation also occurs. We aimed to test these ideas in the montane grasslands of Mount Cameroon, using *Hypericum revolutum* (Hypericaceae) as our model. We gathered data on flower visitors across four elevations and during two distinct seasons. Additionally, given that *Cinnyris reichenowi*, the primary bird visitor of our focal plant species, exhibits sexual dimorphism, our objective was to examine potential differences in bird visitation between sexes. Our results demonstrate a hump-shaped pattern in the relationship between bird floral visitation and elevation, reaching its peak at approximately 2,700 m. a.s.l., with increased frequencies observed during the transition from the wet to dry seasons. Moreover, we found that male *C. reichenowi* exhibited a higher visitation rate to our target plant species compared to females. Additionally, our study confirms an altitude-driven transition from bees to flies as pollinators along the elevation gradient.

Conclusions

Despite our predictions of sunbird-plant interactions being driven by niche-based processes, we found that sunbird-plant networks are structured by both types of processes analysed (**Chapter I**). In this sense, niche-based processes raised in importance during the wet season manifesting the high dynamism present in this system. Consequently, it is the wet season that exerts a higher selective pressure for the traits of each interacting partner to be more attuned to each other. In addition, the relationship between bill and corolla tube length seems to be an important factor in structuring these networks, highlighting that not all traits are equally important.

Moreover, convergent evolutionary processes among bird flower visitors enabled birds with distinct evolutionary trajectories to pollinate plants with which they had not had a tight coevolution (**Chapter II**). Despite the lack of a shared coevolutionary history, these results confirm the bird pollination syndrome as a predictive framework of flower visitors. Nonetheless, this concept should be taken cautiously as a consequence of the highly asymmetrical relationship between plants and their bird flower visitors. We have demonstrated that the ornithophily of a plant species is not enough for it to be more visited by sunbirds (**Chapter III**), but rather associative learning processes related to higher nectar rewards are behind the observed patterns (**Chapter IV**). We emphasize that the bird pollination syndrome concept is a good predictor of bird visitors from the plant's point of view, whereas birds only care for higher nectar rewards.

Additionally, we have shown that despite the great variety of traits displayed by all sunbird species there seems to be a high degree of niche overlap among them (**Chapters I & V**). Perhaps, niche segregation happens at finer scales, as is the case for *Impatiens* species living on the forest elevational gradient, which segregate their pollen deposition sites on their bird visitors. Niche segregation only arises when comparing pairs of species, to one another as was the case of **Chapters I**, and **II**. However, when considering all sunbird species together this pattern is likely obscured by the presence of certain hub plant species across the elevational gradient, as was shown in **Chapters I, IV** and **VI**. Nonetheless, we have demonstrated that sunbird-plant interactions can be as specialised as their New World counterparts (**Chapter VI**). Previous studies on sunbirds from tropical Africa only focused on the interactions during the dry season and at high elevations. Our study was the first one to give a complete picture of how spatiotemporal variability affects sunbird-plant networks in the Afrotropics. **Chapter VI** proved that wet season networks were more specialised, and that high altitude networks were more generalised. In this sense, our results align with that predicted by the altitudinal niche-breadth hypothesis in pollination networks.

Next, we examined the sexual differences in visitation behaviour exhibited by the Vulcano sunbirds (**Chapter V**). The results of this chapter are in line with those shown in **Chapter I**, as we did not find any niche differences related to bill-tube length trait-matching. Moreover, we could not confirm our initial hypothesis of trait-matching related to the higher energetic requirements of male visitors. Again, certain non-ornithophilous plants attracted most bird visitors across the elevational gradient. What we observed was a spatial separation of feeding grounds between males and females. Female individuals migrate downwards during the wet season, likely due to competitive exclusion exerted by males. Territorial behaviour is well-known for nectar-feeding birds as demonstrated by Cotton (1998) and Justino et al. (2012). This phenomenon could also explain the lower visitation frequencies and probabilities of females found in **Chapter VII.** This poses important implications for the conservation of the species as they rely on resources present in several habitats. Moreover, in the face of global change, the species has the risk of mismatching with the flowering of their floral resources. On the other hand, it is noteworthy to mention the ability of nectarivorous birds to adapt to anthropogenic environments as showcased in **Chapter II**.

Finally, we want to emphasize the effect of spatiotemporal variability of the environment as a modulating agent not only of sunbird-plant interactions but of flower visitors in general. This variability has a differential effect among pollinator functional groups, which in turn makes their distributions vary spatiotemporally. Consequently, this poses a selective pressure on plant species to locally adapt to the main floral visitor. This in turn will create speciation events via pollinator-mediated selection processes (i.e., mosaic of coevolution theory in plant-pollinator interactions; Anderson & Johnson, 2007).

To conclude, this dissertation has proven the high asymmetry of sunbird-plant interactions. In this sense, the bird pollination syndrome concept, although still valid should be taken cautiously. From the plant’s point of view, certain traits seem to have more importance than others, namely corolla tube length and the amount of offered reward. Certainly, the interactions seem to be not as tight as previously thought, with periods that drive the evolution of trait-matching among the interacting partners. In this respect, convergent evolutionary processes seem to be enough for the interactions to happen. Moreover, this dissertation has given insights into the high levels of dynamism of the studied systems. This was manifested in the different structural features shown by sunbird-plant interaction networks in response to environmental conditions (i.e., elevation and seasonality). Through the manuscripts and published papers included in this thesis, I also provide insights from a rather understudied biodiversity hotspot in the West African Guinea Forest (i.e., Mount Cameroon). In the future, it will be interesting to see how the patterns and processes found in this thesis affect other aspects of plant ecology, such as plant population structure and distribution.

3. REFERENCES

Abrahamczyk, S., & Kessler, M. (2010). Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. *Journal of Ornithology*, *151*(3), 615–625. https://doi.org/10.1007/s10336-010-0496-x

Abrahamczyk, S., Lozada-Gobilard, S., Ackermann, M., Fischer, E., Krieger, V., Redling, A., & Weigend, M. (2017). A question of data quality—Testing pollination syndromes in Balsaminaceae. *PLOS ONE*, *12*(10), e0186125. https://doi.org/10.1371/journal.pone.0186125

Abrahamczyk, S., & Renner, S. S. (2015). The temporal build-up of hummingbird/plant mutualisms in North America and temperate South America. *BMC Evolutionary Biology*, *15*(1), 104. https://doi.org/10.1186/s12862-015-0388-z

Adedoja, O. A., Kehinde, T., & Samways, M. J. (2018). Insect-flower interaction networks vary among endemic pollinator taxa over an elevation gradient. *PLOS ONE*, *13*(11), e0207453. https://doi.org/10.1371/journal.pone.0207453

Altshuler, D. L. (2003). Flower Color, Hummingbird Pollination, and Habitat Irradiance in Four Neotropical Forests. *Biotropica*, *35*(3), 344–355. https://doi.org/10.1111/j.1744-7429.2003.tb00588.x

Anderson, B., & Johnson, S. D. (2007). The geographical mosaic of coevolution in a plant-pollinator mutualism. *Evolution*, *62*(1), 220–225. https://doi.org/10.1111/j.1558-5646.2007.00275.x

Armbruster, W. S. (2014). Floral specialization and angiosperm diversity: Phenotypic divergence, fitness trade-offs and realized pollination accuracy. *AoB PLANTS*, *6*. https://doi.org/10.1093/aobpla/plu003

Armbruster, W. S., Fenster, C. B., & Dudash, M. R. (2000). Pollination 'Principles' Revisited: Specialization, pollination Syndromes, and the Evolution of FLowers. *The Scadianavian Association for Pollination Ecology Honours Knut Faegri*, *39*, 179–194.

Asar, Y., Ho, S. Y. W., & Sauquet, H. (2022). Early diversifications of angiosperms and their insect pollinators: Were they unlinked? *Trends in Plant Science*, *27*(9), 858–869. https://doi.org/10.1016/j.tplants.2022.04.004

Ashworth, L., Aguilar, R., Martén-Rodríguez, S., Lopezaraiza-Mikel, M., Avila-Sakar, G., Rosas-Guerrero, V., & Quesada, M. (2015). Pollination Syndromes: A Global Pattern of Convergent Evolution Driven by the Most Effective Pollinator. In P. Pontarotti (Ed.), *Evolutionary Biology: Biodiversification from Genotype to Phenotype* (pp. 203–224). Springer International Publishing. https://doi.org/10.1007/978-3-319-19932-0_11

Baker, H. G. (1978): Chemical aspects of the pollination biology of woody plants in the tropics. In: Tomlinson, P. B., & Zimmermann, M. H. (eds.): Tropical trees as living systems. Cambridge University Press, New York, 57-82

Barba-Montoya, J., Dos Reis, M., Schneider, H., Donoghue, P. C. J., & Yang, Z. (2018). Constraining uncertainty in the timescale of angiosperm evolution and the veracity of a

Cretaceous Terrestrial Revolution. *New Phytologist*, *218*, 819–834. https://doi.org/10.1111/nph.15011

Barreto, E., Boehm, M. M. A., Ogutcen, E., Abrahamczyk, S., Kessler, M., Bascompte, J., Dellinger, A. S., Bello, C., Dehling, D. M., Duchenne, F., Kaehler, M., Lagomarsino, L. P., Lohmann, L. G., Maglianesi, M. A., Morlon, H., Muchhala, N., Ornelas, J. F., Perret, M., Salinas, N. R., … Graham, C. H. (2024). Macroevolution of the plant–hummingbird pollination system. *Biological Reviews*, brv.13094. https://doi.org/10.1111/brv.13094

Bartoš, M., & Janeček, Š. (2014). Pollinator-induced twisting of flowers sidesteps floral architecture constraints. *Current Biology*, *24*(17), R793–R795. https://doi.org/10.1016/j.cub.2014.07.056

Bartoš, M., Janeček, Š., Padyšáková, E., Patáčová, E., Altman, J., Pešata, M., Kantorová, J., & Tropek, R. (2012). Nectar properties of the sunbird-pollinated plant Impatiens sakeriana: A comparison with six other co-flowering species. *South African Journal of Botany*, *78*, 63–74. https://doi.org/10.1016/j.sajb.2011.05.015

Bartoš, M., Tropek, R., Spitzer, L., Padyšáková, E., Janšta, P., Straka, J., Tkoč, M., & Janeček, Š. (2015). Specialization of pollination systems of two co-flowering phenotypically generalized Hypericum species (Hypericaceae) in Cameroon. *Arthropod-Plant Interactions*, *9*(3), 241–252. https://doi.org/10.1007/s11829-015-9378-8

Benton, M. J., Wilf, P., & Sauquet, H. (2022). The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. *New Phytologist*, *233*(5), 2017–2035. https://doi.org/10.1111/nph.17822

Blüthgen, N., & Klein, A.-M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant–pollinator interactions. *Basic and Applied Ecology*, *12*(4), 282–291. https://doi.org/10.1016/j.baae.2010.11.001

Blüthgen, N., Menzel, F., & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, *6*(1), 9. https://doi.org/10.1186/1472-6785-6-9

Boles, W. E. (2005). Fossil honeyeaters (Meliphagidae) from the Late Tertiary of Riversleigh, north-western Queensland. *Emu - Austral Ornithology*, *105*(1), 21–26. https://doi.org/10.1071/MU03024

Bolten, A. B., & Feinsinger, P. (1978). Why Do Hummingbird Flowers Secrete Dilute Nectar? *Biotropica*, *10*(4), 307. https://doi.org/10.2307/2387684

Brown, J. H., Calder, W. A., & Kodric-Brown, A. (1978). Correlates and Consequences of Body Size in Nectar-Feeding Birds. *American Zoologist*, *18*(4), 687–738. https://doi.org/10.1093/icb/18.4.687

Buggs, R. J. A. (2021). The origin of Darwin's "abominable mystery". *American Journal of Botany*, *108*(1), 22–36. https://doi.org/10.1002/ajb2.1592

Cardinal, S., & Danforth, B. N. (2013). Bees diversified in the age of eudicots. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1755), 20122686. https://doi.org/10.1098/rspb.2012.2686

Carnicer, J., Jordano, P., & Melián, C. J. (2009). The temporal dynamics of resource use by frugivorous birds: A network approach. *Ecology*, *90*(7), 1958–1970. https://doi.org/10.1890/07-1939.1

Castellanos, M. C., Wilson, P., & Thomson, J. D. (2003). Pollen Transfer by Hummingbirds and Bumblebees, and the Divergence of Pollination Modes in Penstemon. *Evolution*, *57*(12), 2742–2752. https://www.jstor.org/stable/3448727

Chmel, K., Ewome, F. L., Gómez, G. U., Klomberg, Y., Mertens, J. E. J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective. *Oikos*, *130*(8), 1411–1424. https://doi.org/10.1111/oik.08052

Classen, A., Eardley, C. D., Hemp, A., Peters, M. K., Peters, R. S., Ssymank, A., & Steffan-Dewenter, I. (2020). Specialization of plant–pollinator interactions increases with temperature at Mt. Kilimanjaro. *Ecology and Evolution*, *10*(4), 2182–2195. https://doi.org/10.1002/ece3.6056

Collins, B. G., & Rebelo, T. (1987). Pollination biology of the Proteaceae in Australia and southern Africa. *Australian Journal of Ecology*, *12*(4), 387–421. https://doi.org/10.1111/j.1442-9993.1987.tb00958.x

Cotton, P. A. (1998). Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis*, *140*(4), 647–653. https://doi.org/10.1111/j.1474-919X.1998.tb04710.x

Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and molecular context. *Journal of Experimental Botany*, *59*(4), 715–727. https://doi.org/10.1093/jxb/ern009

Cruden, R. W. (1972). Pollinators in High-Elevation Ecosystems: Relative Effectiveness of Birds and Bees. *Science*, *176*(4042), 1439–1440. https://doi.org/10.1126/science.176.4042.1439

Cuartas-Hernández, S. E., Moreno-Betancur, D. J., Gibernau, M., Herrera-Palma, M., & Hoyos-Serna, L. (2019). Contrasting Patterns of Floral Size Variation in Two Sympatric Species of Anthurium along an Elevation Gradient in a Tropical Mountain Forest. *International Journal of Plant Sciences*, *180*(3).

Danieli-Silva, A., Tesserolli de Souza, J. M., Donatti, A. julia, Pamplona Campos, R., Vicente-Silva, J., Freitas, L., & Varassin, I. G. (2012). Do pollination syndromes cause modularity and predict interactions in a pollination network in tropical high-altitude grasslands? *Oikos*, *121*, 35–43. https://doi.org/10.1111/j.1600-0706.2011.19089.x

Del Rio, C. M., & Karasov, W. H. (1990). Digestion Strategies in Nectar- and Fruit-Eating Birds and the Sugar Composition of Plant Rewards. *The American Naturalist*, *136*(5), 618–637. https://doi.org/10.1086/285119

Dellinger, A. S. (2020). Pollination syndromes in the 21st century: Where do we stand and where may we go? *New Phytologist*, *228*(4), 1193–1213. https://doi.org/10.1111/nph.16793

Dellinger, A. S., Hamilton, A. M., Wessinger, C. A., & Smith, S. D. (2023). Opposing Patterns of Altitude-Driven Pollinator Turnover in the Tropical and Temperate Americas. *The American Naturalist*, *202*(2), 152–165. https://doi.org/10.1086/725017

Dellinger, A. S., Pérez-Barrales, R., Michelangeli, F. A., Penneys, D. S., Fernández-Fernández, D. M., & Schönenberger, J. (2021). Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains. *New Phytologist*, *231*(2), 864–877. https://doi.org/10.1111/nph.17390

Dupont, Y. L., Hansen, D. M., & Olesen, J. M. (2003). Structure of a plant – flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*, *26*, 301–310. https://doi.org/10.1034/j.1600-0587.2003.03443.x

Fægri, K., & Pijl, L. V. D. (1979). Applied Pollination Ecology. In K. Fægri & L. V. D. Pijl (Eds.), Principles of Pollination Ecology (Third Edition) (Third Edition, pp. 159–163). Pergamon. https://doi.org/10.1016/B978-0-08-023160-0.50020-7

Feinsinger, P., & Colwell, R. K. (1978). Community Organization Among Neotropical Nectar-Feeding Birds. *American Zoologist*, *18*(4), 779–795. https://doi.org/10.1093/icb/18.4.779

Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination Syndromes and Floral Specialization. *Annual Review of Ecology, Evolution, and Systematics*, *35*(1), 375–403. https://doi.org/10.1146/annurev.ecolsys.34.011802.132347

Fleming, P. A., & Moore, T. L. (2012). Do experimental methods affect estimates of pollen digestion by birds? In *Australian Journal of Zoology* (Vol. 59, Issue 6, pp. 407–415).

Fleming, T. H., Geiselman, C., & Kress, W. J. (2009). The evolution of bat pollination: A phylogenetic perspective. *Annals of Botany*, *104*(6), 1017–1043. https://doi.org/10.1093/aob/mcp197

Foster, C. S. P., Sauquet, H., Van Der Merwe, M., McPherson, H., Rossetto, M., & Ho, S. Y. W. (2017). Evaluating the Impact of Genomic Data and Priors on Bayesian Estimates of the Angiosperm Evolutionary Timescale. *Systematic Biology*, syw086. https://doi.org/10.1093/sysbio/syw086

Gonzalez, O., & Loiselle, B. A. (2016). Species interactions in an Andean bird–flowering plant network: Phenology is more important than abundance or morphology. *PeerJ*, *4*, e2789. https://doi.org/10.7717/peerj.2789

González-Castro, A., Yang, S., Nogales, M., & Carlo, T. A. (2012). What Determines the Temporal Changes of Species Degree and Strength in an Oceanic Island Plant-Disperser Network? *PLoS ONE*, *7*(7), e41385. https://doi.org/10.1371/journal.pone.0041385

Guimarães Jr, P. R., Jordano, P., & Thompson, J. N. (2011). Evolution and coevolution in mutualistic networks. *Ecology Letters*, *14*(9), 877–885. https://doi.org/10.1111/j.1461-0248.2011.01649.x

Hoiss, B., Krauss, J., & Steffan-Dewenter, I. (2015). Interactive effects of elevation, species richness and extreme climatic events on plant-pollinator networks. *Global Change Biology*, *21*(11), 4086–4097. https://doi.org/10.1111/gcb.12968

Hořák, D., & Janeček, Š. (2021). A geographical perspective on the relationship between Impatiens spur lengths and bill lengths of sunbirds in Afrotropical mountains. *Ecology and Evolution*, *11*, 3120–3129. https://doi.org/10.1002/ ece3.7258

Hu, S., Dilcher, D. L., Jarzen, D. M., & Winship Taylor, D. (2008). Early steps of angiosperm–pollinator coevolution. *Proceedings of the National Academy of Sciences*, *105*(1), 240–245. https://doi.org/10.1073/pnas.0707989105

Huang, Z.-H., Song, Y.-P., & Huang, S.-Q. (2017). Evidence for passerine bird pollination in Rhododendron species. *AoB PLANTS*, *9*(6). https://doi.org/10.1093/aobpla/plx062

Janeček, Š., Bartoš, M., & Njabo, K. Y. (2015). Convergent evolution of sunbird pollination systems of *Impatiens* species in tropical Africa and hummingbird systems of the New World: Bird pollination of *Impatiens* species. *Biological Journal of the Linnean Society*, *115*(1), 127–133. https://doi.org/10.1111/bij.12475

Janeček, Š., Chmel, K., Ewome, F. L., Hrubá, K., Klomberg, Y., Kobe, I. N., Kouede, R. D., Mertens, J. E. J., Njie, M. M., & Tropek, R. (2021). Differences in Nectar Traits between Ornithophilous and Entomophilous Plants on Mount Cameroon. *Plants*, *10*(6), 1161. https://doi.org/10.3390/plants10061161

Janeček, Š., Chmel, K., Uceda-Gómez, G., Janečková, P., Chmelová, E., Sejfová, Z., & Ewome, F. L. (2020). Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution*, *10*, 1784–1793. https://doi.org/DOI: 10.1002/ece3.5942

Janeček, Š., Hrázský, Z., Bartoš, M., Brom, J., Reif, J., Hořák, D., Bystřická, D., Riegert, J., Sedláček, O., & Pešata, M. (2007). Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa. *African Journal of Ecology*, *45*(4), 607–613. https://doi.org/10.1111/j.1365-2028.2007.00779.x

Janeček, Š., Riegert, J., Sedláček, O., Bartoš, M., Hořák, D., Reif, J., Padyšáková, E., Fainová, D., Antczak, M., Pešata, M., Mikeš, V., Patáčová, E., Altman, J., Kantorová, J., Hrázský, Z., Brom, J., & Doležal, J. (2012). Food selection by avian floral visitors: An important aspect of plant-flower visitor interactions in West Africa. *Biological Journal of the Linnean Society*, *107*(2), 355–367. https://doi.org/10.1111/j.1095-8312.2012.01943.x

Janzen, D. H. (1980). When is it Coevolution? *Evolution*, *34*(3), 611–612.

Janzen, D. H. (1985). On Ecological Fitting. *Oikos*, *45*(3), 308. https://doi.org/10.2307/3565565

Johnson, S. D., & Nicolson, S. W. (2008). Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biology Letters*, *4*(1), 49–52. https://doi.org/10.1098/rsbl.2007.0496

Jordano, P., Bascompte, J., & Olesen, J. M. (2006). The ecological Consequences of Complex Topology and Nested Structure in Pollinatin Webs. In *Plant-pollinator interactions: From specialization to generalization*. University of Chicago Press.

Justino, D. G., Maruyama, P. K., & Oliveira, P. E. (2012). Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *Journal of Ornithology*, *153*(1), 189–197. https://doi.org/10.1007/s10336-011-0726-x

Kessler, M., Abrahamczyk, S., & Krömer, T. (2020). The role of hummingbirds in the evolution and diversification of Bromeliaceae: Unsupported claims and untested hypotheses. *Botanical Journal of the Linnean Society*, *192*(4), 592–608. https://doi.org/10.1093/botlinnean/boz100

Klomberg, Y., Tropek, R., Mertens, J. E. J., Kobe, I. N., Hodeček, J., Raška, J., Fominka, N. T., Souto-Vilarós, D., Janečková, P., & Janeček, Š. (2022). Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. *Ecology Letters*, *25*(4), 839–850. https://doi.org/10.1111/ele.13958

Köhler, A., Leseigneur, C. D. C., Verburgt, L., & Nicolson, S. W. (2010). Dilute bird nectars: Viscosity constrains food intake by licking in a sunbird. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology*, *299*(4), R1068–R1074. https://doi.org/10.1152/ajpregu.00208.2010

Krauss, S. L., Phillips, R. D., Karron, J. D., Johnson, S. D., Roberts, D. G., & Hopper, S. D. (2017). Novel Consequences of Bird Pollination for Plant Mating. *Trends in Plant Science*, *22*(5), 395–410. https://doi.org/10.1016/j.tplants.2017.03.005

Kuriya, S., Hattori, M., Nagano, Y., & Itino, T. (2015). Altitudinal flower size variation correlates with local pollinator size in a bumblebee-pollinated herb, *Prunella vulgaris* L. (Lamiaceae). *Journal of Evolutionary Biology*, *28*(10), 1761–1769. https://doi.org/10.1111/jeb.12693

Labandeira, C. C. (2010). The Pollination of Mid Mesozoic Seed Plants and the Early History of Long-proboscid Insects. *Annals of the Missouri Botanical Garden*, *97*(4), 469–513. https://doi.org/10.3417/2010037

Lagomarsino, L. P., Forrestel, E. J., Muchhala, N., & Davis, C. C. (2017). Repeated evolution of vertebrate pollination syndromes in a recently diverged Andean plant clade. *Evolution*, *71*(8), 1970–1985. https://doi.org/10.1111/evo.13297

Lay, C. R., Linhart, Y. B., & Diggle, P. K. (2013). Variation among Four Populations of Erysimum Capitatum in Phenotype, Pollination and Herbivory over an Elevational Gradient. *The American Midland Naturalist*, *169*(2), 259–273. https://doi.org/10.1674/0003-0031-169.2.259

Lefebvre, V., Villemant, C., Fontaine, C., & Daugeron, C. (2018). Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. *Scientific Reports*, *8*(1), 4706. https://doi.org/10.1038/s41598-018-23210-y

Lehmann, L. J., Maruyama, P. K., Joaquim Bergamo, P., Maglianesi, M. A., Rahbek, C., & Dalsgaard, B. (2019). Relative effectiveness of insects *versus* hummingbirds as pollinators of Rubiaceae plants across elevation in Dominica, Caribbean. *Plant Biology*, *21*(4), 738–744. https://doi.org/10.1111/plb.12976

Li, H.-T., Yi, T.-S., Gao, L.-M., Ma, P.-F., Zhang, T., Yang, J.-B., Gitzendanner, M. A., Fritsch, P. W., Cai, J., Luo, Y., Wang, H., Van Der Bank, M., Zhang, S.-D., Wang, Q.-F., Wang, J., Zhang, Z.-R., Fu, C.-N., Yang, J., Hollingsworth, P. M., … Li, D.-Z. (2019). Origin of angiosperms and the puzzle of the Jurassic gap. *Nature Plants*, *5*(5), 461–470. https://doi.org/10.1038/s41477-019-0421-0

Magallón, S., Gómez-Acevedo, S., Sánchez-Reyes, L. L., & Hernández-Hernández, T. (2015). A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist*, *207*, 437–453. https://doi.org/10.1111/nph.13264

Maglianesi, M. A., Blüthgen, N., Böhning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics. *Ecology*, *95*(12), 3325–3334. https://doi.org/10.1890/13-2261.1

Maglianesi, M. A., Böhning-Gaese, K., & Schleuning, M. (2015). Different foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant–pollinator interactions. *Journal of Animal Ecology*, *84*(3), 655–664. https://doi.org/10.1111/1365-2656.12319

Maguiña-Conde, R., Zuñiga-Rivas, D., & Kay, K. M. (2023). An elevational gradient in floral traits and pollinator assemblages in the Neotropical species Costus guanaiensis var. Tarmicus in Peru. *Ecology and Evolution*, *13*(8), 1–18. https://doi.org/10.1002/ece3.10314

Maicher, V., Sáfián, S., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., Kobe, I. N., Janeček, Š., Mertens, J. E. J., Fokam, E. B., Pyrcz, T., Doležal, J., Altman, J., Hořák, D., Fiedler, K., & Tropek, R. (2020). Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *Journal of Biogeography*, *47*(2), 342–354. https://doi.org/10.1111/jbi.13740

Martén-Rodríguez, S., Almarales-Castro, A., & Fenster, C. B. (2009). Evaluation of pollination syndromes in Antillean Gesneriaceae: Evidence for bat, hummingbird and generalized flowers. *Journal of Ecology*, *97*(2), 348–359. https://doi.org/10.1111/j.1365-2745.2008.01465.x

Maruyama, P. K., Vizentin-Bugoni, J., Oliveira, G. M., Oliveira, P. E., & Dalsgaard, B. (2014). Morphological and Spatio-Temporal Mismatches Shape a Neotropical Savanna Plant-Hummingbird Network. *Biotropica*, *46*(6), 740–747. https://doi.org/10.1111/btp.12170

Mayr, G. (2004). Old World Fossil Record of Modern-Type Hummingbirds. *Science*, *304*(5672), 861–864. https://doi.org/10.1126/science.1096856

McCabe, L. M., & Cobb, N. S. (2021). From Bees to Flies: Global Shift in Pollinator Communities Along Elevation Gradients. *Frontiers in Ecology and Evolution*, *8*, 626124. https://doi.org/10.3389/fevo.2020.626124

Mertens, J. E. J., Janeček, Š., Dzekashu, F. F., Chmelová, E., Fokam, E. B., & Tropek, R. (2020). Changes in pollinator community of Scadoxus cinnabarinus (Amaryllidaceae) along its elevational range on Mount Cameroon. *Arthropod-Plant Interactions*, *14*(2), 215–226. https://doi.org/10.1007/s11829-020-09741-0

Muchala, N. (2007). *Adaptive Trade-Off in Floral Morphology Mediates Specialization for Flowers Pollinated by Bats and Hummingbirds.*

Muchala, N. (2019). Quantum dots shed light on angiosperm speciation. *New Phytologist*, *224*(3), 1005–1008. https://doi.org/10.1111/nph.16211

Nagano, Y., Abe, K., Kitazawa, T., Hattori, M., Hirao, A. S., & Itino, T. (2014). Changes in pollinator fauna affect altitudinal variation of floral size in a bumblebee-pollinated herb. *Ecology and Evolution*, *4*(17), 3395–3407. https://doi.org/10.1002/ece3.1191

Nicolson, S. W. (2007). Nectar consumers. In Nectaries and Nectar (eds S. W. Nicolson, M. Nepi & E. Pacini), pp. 289–342. Springer, Dordrecht

Nie, Y., Foster, C. S. P., Zhu, T., Yao, R., Duchêne, D. A., Ho, S. Y. W., & Zhong, B. (2020). Accounting for Uncertainty in the Evolutionary Timescale of Green Plants Through Clock-Partitioning and Fossil Calibration Strategies. *Systematic Biology*, *69*(1), 1–16. https://doi.org/10.1093/sysbio/syz032

Nsor, C. A., Godsoe, W., & Chapman, H. M. (2019). Promiscuous pollinators—Evidence from an Afromontane sunbird–plant pollen transport network. *Biotropica*, *51*(4), 538–548. https://doi.org/10.1111/btp.12669

Olesen, J. M., & Valido, A. (2003). Lizards as pollinators and seed dispersers: An island phenomenon. *Trends in Ecology & Evolution*, *18*(4), 177–181. https://doi.org/10.1016/S0169-5347(03)00004-1

Ollerton, J. (2003). The Pollination Ecology of an Assemblage of Grassland Asclepiads in South Africa. *Annals of Botany*, *92*(6), 807–834. https://doi.org/10.1093/aob/mcg206

Ollerton, J. (2017). Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 353–376. https://doi.org/10.1146/annurev-ecolsys-110316-022919

Ollerton, J. (2024). *Birds and Flowers: An Intimate 50 Million Year Relationship*. Pelagic Publishing.

Ollerton, J., Alarcón, R., Waser, N. M., Price, M. V., Watts, S., Cranmer, L., Hingston, A., Peter, C. I., & Rotenberry, J. (2009). A global test of the pollination syndrome hypothesis. *Annals of Botany*, *103*(9), 1471–1480. https://doi.org/10.1093/aob/mcp031

Opedal, Ø. H. (2019). The evolvability of animal-pollinated flowers: Towards predicting adaptation to novel pollinator communities. *New Phytologist*, *221*, 1128–1135. https://doi.org/10.1111/nph.15403

Padyšáková, E., Bartoš, M., Tropek, R., & Janeček, Š. (2013). Generalization versus Specialization in Pollination Systems: Visitors, Thieves, and Pollinators of *Hypoestes aristata* (Acanthaceae). *Plo One*, *8*(4), e59299. https://doi.org/doi:10.1371/journal.pone.0059299

Partida-Lara, R., Enríquez, P. L., Vázquez-Pérez, J. R., De Bonilla, E. P.-D., Martínez-Ico, M., & Rangel-Salazar, J. L. (2018). Pollination syndromes and interaction networks in hummingbird assemblages in El Triunfo Biosphere Reserve, Chiapas, Mexico. *Journal of Tropical Ecology*, *34*(5), 293–307. https://doi.org/10.1017/S0266467418000263

Paw, A. (2006). Floral syndromes accurately predict pollination by a specialized oil-collecting bee (Rediviva peringueyi) in a guild of south African orchids (Coryciinae. *American Journal of Botany*, *93*(6), 917–926. https://doi.org/10.3732/ajb.93.6.917

Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E., & Gravel, D. (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, *93*(2), 785–800. https://doi.org/10.1111/brv.12366

Peñalver, E., Arillo, A., Pérez-de la Fuente, R., Riccio, M. L., Delclòs, X., Barrón, E., & Grimaldi, D. A. (2015). Long-Proboscid Flies as Pollinators of Cretaceous Gymnosperms. *Current Biology*, *25*(14), 1917–1923. https://doi.org/10.1016/j.cub.2015.05.062

Pi, H. Q., Quan, Q.-M., Wu, B., Lv, X.-W., Shen, L.-M., & Huang, S.-Q. (2021). Altitude-related shift of relative abundance from insect to sunbird pollination in Elaeagnus umbellata (Elaeagnaceae). *Journal of Systematics and Evolution*, *59*(6), 1266–1275. https://doi.org/doi: 10.1111/jse.12685

Proctor, M., Yeo, P., & Lack, A. (1996). *The Natural History of Pollination*.

Ramírez, S. R., Eltz, T., Fujiwara, M. K., Gerlach, G., Goldman-Huertas, B., Tsutsui, N. D., & Pierce, N. E. (2011). Asynchronous Diversification in a Specialized Plant-Pollinator Mutualism. *Science*, *333*(6050), 1742–1746. https://doi.org/10.1126/science.1209175

Ramírez-Barahona, S., Sauquet, H., & Magallón, S. (2020). The delayed and geographically heterogeneous diversification of flowering plant families. *Nature Ecology & Evolution*, *4*(9), 1232–1238. https://doi.org/10.1038/s41559-020-1241-3

Rasmann, S., Alvarez, N., & Pellissier, L. (2014). The Altitudinal Niche-Breadth Hypothesis in Insect-Plant Interactions. In C. Voelckel & G. Jander (Eds.), *Annual Plant Reviews* (pp. 339–359). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781118829783.ch10

Regan, E. C., Santini, L., Ingwall-King, L., Hoffmann, M., Rondinini, C., Symes, A., Taylor, J., & Butchart, S. H. M. (2015). Global Trends in the Status of Bird and Mammal Pollinators. *Conservation Letters*, *8*(6), 397–403. https://doi.org/10.1111/conl.12162

Ren, D., Labandeira, C. C., Santiago-Blay, J. A., Rasnitsyn, A., Shih, C., Bashkuev, A., Logan, M. A. V., Hotton, C. L., & Dilcher, D. (2009). A Probable Pollination Mode Before Angiosperms: Eurasian, Long-Proboscid Scorpionflies. *Science*, *326*(5954), 840–847. https://doi.org/10.1126/science.1178338

Richardson, K., & Wooller, R. (1986). The Structures of the Gastrointestinal Tracts of Honeyeaters and Other Small Birds in Relation to Their Diets. *Australian Journal of Zoology*, *34*(2), 119–124.

Rico-Guevara, A., & Rubega, M. A. (2011). The hummingbird tongue is a fluid trap, not a capillary tube. *Proceedings of the National Academy of Sciences*, *108*(23), 9356–9360. https://doi.org/10.1073/pnas.1016944108

Rosas-Guerrero, V., Aguilar, R., Rodríguez, S. M., Ashworth, L., Lopezaraiza-Mikel, M., & Quesada, M. (2014). A quantitative review of pollination syndromes: Do floral traits predict effective pollinators? *Ecology Letters*, *17*, 388–400. https://doi.org/doi: 10.1111/ele.12224

Salomo, K., Smith, J. F., Feild, T. S., Samain, M.-S., Bond, L., Davidson, C., Zimmers, J., Neinhuis, C., & Wanke, S. (2017). The Emergence of Earliest Angiosperms May be Earlier than Fossil Evidence Indicates. *Systematic Botany*, *42*(4), 607–619. https://doi.org/10.1600/036364417X696438

Santamaría, L., & Rodríguez-Gironés, M. A. (2007). Linkage Rules for Plant–Pollinator Networks: Trait Complementarity or Exploitation Barriers? *PLoS Biology*, *5*(2), e31. https://doi.org/10.1371/journal.pbio.0050031

Santiago-Hernández, M. H., Martén-Rodríguez, S., Lopezaraiza-Mikel, M., Oyama, K., González-Rodríguez, A., & Quesada, M. (2019). The role of pollination effectiveness on the attributes of interaction networks: From floral visitation to plant fitness. *Ecology*, *100*(10), e02803. https://doi.org/10.1002/ecy.2803

Sauquet, H., Ramírez-Barahona, S., & Magallón, S. (2022). What is the age of flowering plants? *Journal of Experimental Botany*, *73*(12), 3840–3853. https://doi.org/10.1093/jxb/erac130

Sauquet, H., Von Balthazar, M., Magallón, S., Doyle, J. A., Endress, P. K., Bailes, E. J., Barroso De Morais, E., Bull-Hereñu, K., Carrive, L., Chartier, M., Chomicki, G., Coiro, M., Cornette, R., El Ottra, J. H. L., Epicoco, C., Foster, C. S. P., Jabbour, F., Haevermans, A., Haevermans, T., … Schönenberger, J. (2017). The ancestral flower of angiosperms and its early diversification. *Nature Communications*, *8*(1), 16047. https://doi.org/10.1038/ncomms16047

Sazatornil, F. D., Moré, M., Benitez-Vieyra, S., Cocucci, A. A., Kitching, I. J., Schlumpberger, B. O., Oliveira, P. E., Sazima, M., & Amorim, F. W. (2016). Beyond neutral and forbidden links: Morphological matches and the assembly of mutualistic hawkmoth–plant networks. *Journal of Animal Ecology*, *85*(6), 1586–1594. https://doi.org/10.1111/1365-2656.12509

Schiestl, F. P., & Dötterl, S. (2012). The Evolution of Floral Scent and Olfactory Preferences in Pollinators: Coevolution or Pre-Exisiting Bias? *Evolution*, *66*(7), 2042–2055. https://doi.org/10.1111/j.1558-5646.2012.01593.x

Schmidt-Lebuhn, A. N., Müller, M., Pozo Inofuentes, P., Encinas Viso, F., & Kessler, M. (2019). Pollen analogues are transported across greater distances in bee-pollinated than in hummingbird-pollinated species of *Justicia* (Acanthaceae). *Biotropica*, *51*(2), 99–103. https://doi.org/10.1111/btp.12633

Schweizer, M., Seehausen, O., & Hertwig, S. T. (2011). Macroevolutionary patterns in the diversification of parrots: Effects of climate change, geological events and key innovations: Macroevolutionary patterns in the diversification of parrots. *Journal of Biogeography*, *38*(11), 2176–2194. https://doi.org/10.1111/j.1365-2699.2011.02555.x

Silvestro, D., Bacon, C. D., Ding, W., Zhang, Q., Donoghue, P. C. J., Antonelli, A., & Xing, Y. (2021). Fossil data support a pre-Cretaceous origin of flowering plants. *Nature Ecology & Evolution*, *5*(4), 449–457. https://doi.org/10.1038/s41559-020-01387-8

Silvestro, D., Cascales-Miñana, B., Bacon, C. D., & Antonelli, A. (2015). Revisiting the origin and diversification of vascular plants through a comprehensive Bayesian analysis of the fossil record. *New Phytologist*, *207*(2), 425–436. https://doi.org/10.1111/nph.13247

Snow, B. K., & Snow, D. W. (1972). Feeding Niches of Hummingbirds in a Trinidad Valley. *The Journal of Animal Ecology*, *41*(2), 471. https://doi.org/10.2307/3481

Sommaggio, D., Zanotelli, L., Vettorazzo, E., Burgio, G., & Fontana, P. (2022). Different Distribution Patterns of Hoverflies (Diptera: Syrphidae) and Bees (Hymenoptera: Anthophila) Along Altitudinal Gradients in Dolomiti Bellunesi National Park (Italy). *Insects*, *13*(3), 293. https://doi.org/10.3390/insects13030293

Sonne, J., Zanata, T. B., Martín González, A. M., Cumbicus Torres, N. L., Fjeldså, J., Colwell, R. K., Tinoco, B. A., Rahbek, C., & Dalsgaard, B. (2019). The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. *Biotropica*, *51*(2), 205–218. https://doi.org/10.1111/btp.12637

Specht, C. D., Yockteng, R., Almeida, A. M., Kirchoff, B. K., & Kress, W. J. (2012). Homoplasy, Pollination, and Emerging Complexity During the Evolution of Floral Development in the Tropical Gingers (Zingiberales). *The Botanical Review*, *78*(4), 440–462. https://doi.org/10.1007/s12229-012-9111-6

Stang, M., Klinkhamer, P. G. L., & Van Der Meijden, E. (2007). Asymmetric specialization and extinction risk in plant–flower visitor webs: A matter of morphology or abundance? *Oecologia*, *151*(3), 442–453. https://doi.org/10.1007/s00442-006-0585-y

Stebbins, G. L. (1970). Adaptive Radiation of Reproductive Characteristics in Angiosperms, I: Pollination Mechanisms. *Annual Review of Ecology and Systematics*, *1*(1), 307–326. https://doi.org/10.1146/annurev.es.01.110170.001515

Stephens, R. E., Gallagher, R. V., Dun, L., Cornwell, W., & Sauquet, H. (2023). Insect pollination for most of angiosperm evolutionary history. *New Phytologist*, *240*(2), 880–891. https://doi.org/10.1111/nph.18993

Thompson, J.N. (2005). The geographic mosaic of coevolution. University of Chicago Press, Chicago

Thomson, J. D., & Wilson, P. (2008). Explaining Evolutionary Shifts between Bee and Hummingbird Pollination: Convergence, Divergence, and Directionality. *International Journal of Plant Sciences*, *169*(1), 23–38. https://doi.org/10.1086/523361

Toon, A., Hughes, J. M., & Joseph, L. (2010). Multilocus analysis of honeyeaters (Aves: Meliphagidae) highlights spatio-temporal heterogeneity in the influence of biogeographic barriers in the Australian monsoonal zone. *Molecular Ecology*, *19*, 2980–2994. https://doi.org/doi: 10.1111/j.1365-294X.2010.04730.x

Uceda-Gómez, G**.**, Chmel, K., Janečková, P., Mlíkovský, J., Klomberg, Y., Ewome, F. L., Molua, L. L., Njie, M. M., Tropek, R., & Janeček, Š. (2024). Drivers of sunbird-plant interactions on Mount Cameroon: Between neutrality and niche-based processes. *Biotropica*, 56, 136–148. https://doi.org/10.1111/btp.13290

Van Der Kooi, C. J., & Ollerton, J. (2020). The origins of flowering plants and pollinators. *Science*, *368*(6497), 1306–1308. https://doi.org/10.1126/science.aay3662

Vasconcelos, T. N. C., Chartier, M., Prenner, G., Martins, A. C., Schönenberger, J., Wingler, A., & Lucas, E. (2019). Floral uniformity through evolutionary time in a species-rich tree lineage. *New Phytologist*, *221*(3), 1597–1608. https://doi.org/10.1111/nph.15453

Vázquez, D. P., Blüthgen, N., Cagnolo, L., & Chacoff, N. P. (2009a). Uniting pattern and process in plant–animal mutualistic networks: A review. *Annals of Botany*, *103*(9), 1445–1457. https://doi.org/10.1093/aob/mcp057

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009b). Evaluating multiple determinants of the structure of plant–animal mutualistic networks. *Ecology*, *90*(8), 2039–2046. https://doi.org/10.1890/08-1837.1

Vizentin-Bugoni, J., Maruyama, P. K., De Souza, C. S., Ollerton, J., Rech, A. R., & Sazima, M. (2018). Plant-Pollinator Networks in the Tropics: A Review. In W. Dáttilo & V. Rico-Gray

(Eds.), *Ecological Networks in the Tropics* (pp. 73–91). Springer International Publishing. https://doi.org/10.1007/978-3-319-68228-0_6

Warren, B. H., Bermingham, E., Bowie, R. C. K., Prys-Jones, R. P., & Thébaud, C. (2003). Molecular phylogeography reveals island colonization history and diversification of western Indian Ocean sunbirds (Nectarinia: Nectariniidae). *Molecular Phylogenetics and Evolution*, *29*(1), 67–85. https://doi.org/10.1016/S1055-7903(03)00063-0

Waser, N. M., Chittka, L., Price, M. V., Williams, N. M., & Ollerton, J. (1996). Generalization in Pollination Systems, and Why it Matters. *Ecology*, *77*(4), 1043–1060. https://doi.org/10.2307/2265575

Wilmer, P. 2011. *Pollination and floral ecology*. Princeton, USA: Princeton University

Press.

Whittall, J. B., & Hodges, S. A. (2007). Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature*, *447*(7145), 706–709. https://doi.org/10.1038/nature05857

Worthy, T. H., Tennyson, A. J. D., & Scofield, R. P. (2011). An early Miocene diversity of parrots (Aves, Strigopidae, Nestorinae) from New Zealand. *Journal of Vertebrate Paleontology*, *31*(5), 1102–1116. https://doi.org/10.1080/02724634.2011.595857

Zanata, T. B., Dalsgaard, B., Passos, F. C., Cotton, P. A., Roper, J. J., Maruyama, P. K., Fischer, E., Schleuning, M., Martín González, A. M., Vizentin-Bugoni, J., Franklin, D. C., Abrahamczyk, S., Alárcon, R., Araujo, A. C., Araújo, F. P., Azevedo-Junior, S. M. De., Baquero, A. C., Böhning-Gaese, K., Carstensen, D. W., Chupil, H., Coelho, A.G., Faria, R.R., Hořák, D., Ingversen, T.T., Janeček, Š, Kohler, G., Lara, C., Las-Casas, F.M., Lopes, A.V., Machado, A.O., Machado, C.G., Machado, I.C., Maglianesi, M.A., Malucelli, T.S., Mohd-Azlan, J., Moura, A.C., Oliveira, G.M., Oliveira, P.E., Ornelas, J.F., Riegert, J., Rodrigues, L., Rosero-Lasprilla, L., Rui, A.M., Sazima, M., Schmid, B., Sedláček, O., Timmermann, A., Vollstadt, M.G.R., Wang, Z., Watts, S., Rahbek, C., & Varassin, I. G. (2017). Global patterns of interaction specialization in bird–flower networks. Journal of Biogeography, 44(8), 1891–1910. https://doi.org/10.1111/jbi.13045

Zhang, L., Chen, F., Zhang, X., Li, Z., Zhao, Y., Lohaus, R., Chang, X., Dong, W., Ho, S. Y. W., Liu, X., Song, A., Chen, J., Guo, W., Wang, Z., Zhuang, Y., Wang, H., Chen, X., Hu, J., Liu, Y., … Tang, H. (2020). The water lily genome and the early evolution of flowering plants. *Nature*, *577*(7788), 79–84. https://doi.org/10.1038/s41586-019-1852-5

PART-I DRIVERS OF SUNBIRD-PLANT POLLINATION INTERACTIONS

Cinnyris reichenowi visiting *Lobelia columnaris*

Chapter I

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ORIGINAL ARTICLE

Drivers of sunbird-plant interactions on Mount Cameroon: Between neutrality and niche-based processes

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Abstract

The drivers behind plant-pollinator interactions still need to be fully understood. Previous research has suggested that observed interactions result from either neutral interaction between species based on their abundance or from niche-based processes, which are reflected in the adaptations of both plants and pollinators. Furthermore, the importance of both scenarios can differ depending on seasonal dynamics translated into differences in resource availability. Extensive research has been conducted on New-World hummingbirds (*Trochilidae*), whereas much less is known about Old World nectar-feeding sunbirds (*Nectariniidae*). Our study aimed to explore whether sunbird-plant interactions are explained by neutral and/or niche-based processes. Thus, we tested the effects of abundance, morphology, and nectar sugar content on the observed interactions and the link between sunbirds and plant traits. Moreover, we explored the effects of robbing on these mechanisms. Finally, we investigated the partitioning of bird pollination niches, based on floral traits. We used a dataset of sunbird-plant interactions collected at Mount Cameroon during two seasons (dry and wet seasons). Our study shows that sunbird-plant interactions are influenced by both neutral and niche-based processes. Neutral processes and nectar reward were the main mechanisms underlaying the observed interactions in the dry season. However, as more ornithophilous plants bloom during the rainy season, morphological trait-matching becomes more important. We found a correlation between bill length and floral tube dimensions and observed niche overlap among the sunbird species. Considering this and other research, we suggest that plant-pollinator interactions are influenced by a combination of both neutral and niche-based processes.

KEYWORDS
Afrotropics, floral traits, *Nectariniidae*, nectarivory, niche overlap, ornithophily, pollination, tropical rainforest

1 | INTRODUCTION

The organization of plant-pollinator communities can be driven by neutral and niche-based processes (Maglianesi et al., 2014; Sonne et al., 2019; Vázquez et al., 2009). These two concepts are not mutually exclusive, and both can influence plant-pollinator interactions (i.e., *continuum hypothesis*; Gravel et al., 2006). According to neutrality, network architecture is a consequence of the random encounters of interacting partners, regardless of their traits (i.e., neutral theory of biodiversity; Dupont et al., 2003; Hubbell, 2001; Ollerton et al., 2003). Thus, abundance is supposed to play a critical role in structuring the networks. Conversely, niche-based processes assume that species interactions are driven by their traits (Stang et al., 2007). For example, *Scadoxus puniceus* flowers match in length with the bills of their sunbird visitors, and their floral nectar properties indicate specialization for sunbird pollination (Butler et al., 2022).

The interactions between nectar-feeding birds and flowering plants are an excellent system for studying these processes. Studies supporting the neutrality concept indicate widespread generalization in bird-plant visitation networks, where many birds visit phenotypically non-specialized plants with easily accessible nectar rewards (Chmel et al., 2021; Maruyama et al., 2014; Nsor et al., 2019). In contrast, the niche-based concept finds support from authors studying the morphological adaptations in birds for nectarivory (Cronk & Ojeda, 2008; Fenster et al., 2004; Geerts & Pauw, 2009) and plants for ornithophily (i.e., bird pollination syndrome; Van der Pijl, 1961; Faegri & van der Pijl, 1979). Maglianesi et al. (2014) demonstrated that trait-matching influences the partitioning of avian feeding niches at the community level. These interspecific associations enable efficient extraction of floral rewards by birds, fostering plant pollination and suggesting close coevolution between interacting partners (Biddick & Burns, 2018; Geerts & Pauw, 2009; Janečková et al., 2020; Johnson et al., 2020; but see Janeček et al., 2020).

Despite these co-adaptations, not all plant and bird traits are equally important for their mutual interactions (Chmel et al., 2021). The correlation between bill and corolla length lowers the foraging costs for hummingbirds by minimizing flower handling time and maximizing resource uptake (Maglianesi et al., 2014; Temeles et al., 2009). Examples of phenotypic trait-matching also originate from the Old World (Hořák & Janeček, 2021). Long-billed *Cyanomitra oritis* visited plants with the longest floral tubes (Janeček et al., 2012). Additionally, Payne et al. (2022) found that the morphological characteristics of *Aloe reitzii* flowers matched those of their specialized visitors. Moreover, the narrow entrance of short-tubed *Aloe* species facilitated pollen deposition on the bill of malachite sunbirds (Hargreaves et al., 2019). Furthermore, flower architecture and dimensions may also influence the preferences of bird visitors (Fenster et al., 2015) and the efficiency with which they extract nectar rewards (Padyšáková & Janeček, 2016; Sejfová et al., 2021).

Nonetheless, morphological trait-mismatching can lead to forbidden links as in network terminology, where the pollinator faces exploitation barriers preventing legitimate access to the nectar rewards (Santamaria & Rodríguez-Girones, 2014; Snow & Snow, 1972). Despite these barriers, birds can bypass them through robbing behavior, piercing the corolla without touching the plant's reproductive organs (e.g., Janeček, Bartoš, & Njabo, 2015). Long and wide flowers are more prone to robbing (Navarro & Medel, 2009; Sakhalkar et al., 2023). However, even when there is trait-matching, visitors may act as robbers (Inouye, 1983). Nectar robbers can negatively affect plant fitness by exhausting nectar, destroying floral tissues (Irwin et al., 2001), or keeping true pollinators away from the flower (Irwin & Brody, 1998; Tropek et al., 2013). Nonetheless, they can also have a positive impact on plant reproduction (Navarro, 2000; Rojas-Nossa et al., 2021).

Apart from addressing trait-mismatching and its consequences, it is essential to consider how the associations between the nectar provided and bird energetic requirements affect bird-plant interactions. Nectarivorous birds have high energy requirements that vary depending on their body size, thermoregulation, foraging behavior, and mode of locomotion (Brown et al., 1978). This variation is reflected in the properties of the chosen reward. The most essential nectar properties associated with animal pollination are nectar volume and sugar concentration. Ornithophilous flowers have a high volume of rather diluted nectar (Chmel et al., 2021; Cronk & Ojeda, 2008; Klomberg et al., 2022). Nectar sugar composition also showed pollinator-dependent variations; sunbird-visited plants exhibited high sucrose to hexose ratios in nectar (Bartoš et al., 2012; Janeček et al., 2021), aligning with the nectar characteristics of plants pollinated by their New-World counterparts (Johnson & Nicolson, 2008).

Additionally, seasonality may also affect plant-pollinator interactions. Climatic conditions favor specific pollinator types; for example, birds are favored under colder and/or wetter conditions when ectothermic insects are less active (Huang et al., 2017; Maicher et al., 2018). Moreover, seasonality influences plant phenological patterns in the tropics, thereby affecting the availability of floral resources. Thus, more ornithophilous plants in flower were reported during the wet season of Mt. Cameroon (Janeček, Bartoš, & Njabo, 2015; Klomberg et al., 2022). Furthermore, sunbird-plant networks were more specialized during the wet season, coinciding with the blossoming of specialized ornithophilous plants (Janeček et al., 2022). Similarly, Partida-Lara et al. (2018) found increased specialization in hummingbird-plant networks when resource availability was lower. Therefore, changes in pollinator groups, resource availability, and plant community traits influence how plants and pollinators interact, ultimately affecting their trait-matching.

Our study examines the factors influencing sunbird-plant interactions and their seasonal variation on Mount Cameroon, a relatively understudied biodiversity hotspot in the West African Guinea forests (Küpper et al., 2004). We investigate the roles of abundance, morphology, and nectar reward in determining the interaction frequency and association between avian and plant traits and their seasonal variation. We studied sunbird-plant pollination interactions at four sampling locations during the wet and dry seasons. We aim to answer the following questions: (i) Are sunbird-plant interactions driven by neutral or niche-based processes? (ii) Is there a seasonal variation in the significance of these drivers? (iii) Do different sunbird species establish distinct functional feeding niches based on the traits of the plants they visit? We hypothesize that sunbird-plant interactions will be driven by niche-based processes. Moreover, we expect that the presence of nectar robbing will obscure these niche-related processes, as this behavior represents the ability to bypass the filtering effect of floral tube lengths. Because the reciprocal adaptations of both interacting partners, we anticipate that bird traits will predict the complex of visited plant traits. Second, we hypothesize that there will be seasonal differences in the importance of these mechanisms. Niche-based processes are stronger during the rainy season, because of the flowering of more ornithophilous flowers. Finally, sunbird feeding niches segregate according to the floral traits of the plants that they visit. We expect them to be more dispersed than expected under null models, in which plants are visited randomly.

2 | METHODS

2.1 | Study sites

This study was conducted on the southwestern slope of Mount Cameroon. Mount Cameroon has complete tropical forest elevational gradient stretching from ~400 m a.s.l. to a timberline at ~2200 m a.s.l. (Cable & Cheek 1998). The data were collected at four sites along this gradient, representing four forest types (Table S1): (a) lowland forest in Drink Garri (650 m a.s.l.), (b) mid-elevation forest in PlanteCam camp (1100 m a.s.l.), (c) submontane forest in Crater Lake (1500 m a.s.l.), and (d) montane forest in Mann's Spring (2200 m a.s.l.). Mount Cameroon presents distinct seasonality (Maicher et al., 2020), with a period of water shortage (mid-November to February) combined with a wet season of heavy rains (June to September). Data were collected during four expeditions in two seasons: twice in the dry and twice in the wet season. Two sites were sampled for each expedition. Six transects (200 m long and 10 m wide, approximately 100 m apart, as described in Klomberg et al., 2022) were established at each site to quantify flower abundance in both seasons and to observe sunbird-plant interactions. We used point counts to estimate bird abundance along the transects (Ralph et al., 1995).

2.2 | Observation of bird-plant interactions

A plant individual was the observational unit. Nonetheless, when distinguishing an individual plant (e.g., lianas and vines) was difficult, we defined an individual as those with flowering parts that were not noticeably connected. To include a plant species in the study, we set a limit of nectar production of at least 0.3 μL of nectar per flower (Janeček et al., 2021). From these, we included all plant species that blossomed in at least three of the six transects per studied site and season and/or were common in the transects' surroundings. Data on sunbird-plant interactions were collected by observation of individual plant specimens (used in Janeček et al., 2022).

2.3 | Trait dataset

Only specialized nectar-feeding sunbirds in our interaction dataset were included in the analyses. The species included were: *Anthodiaeta collaris*, *Anthreptes rectirostris*, *Chalcomitra rubescens*, *Cinnyris batesi*, *Cinnyris johannae*, *Cinnyris minullus*, *Cinnyris reichenowi*, *Cinnyris ursulae*, *Cyanomitra cyanolaema*, *Cyanomitra olivacea*, and *Cyanomitra oritis*. We focused on pollination-related traits. Sunbird species traits were gathered from the AVONET database (Tobias et al., 2022a; Tobias et al., 2022b): bird weight and measures of bill length, depth, and width of each sunbird species (Table S2).

We measured and recorded 11 plant species traits related to floral morphology and pollinator attraction (Table S2; partly used in Klomberg et al., 2022). Morphological traits were length and width (at the entrance) of the floral tube or spur and total flower size. Measurements were taken for up to five plant individuals per species. Additionally, we recorded the floral symmetry of the plant (zygo- and actinomorphy), flower position (horizontal, pendant, upright, all), and anther position (exposed, partially exposed, hidden). To prevent visitors from accessing nectar, we covered 15 or more randomly selected flowers for 24 h. We measured the volume of nectar per flower and the concentration of nectar (w/w %) (used in Janeček et al., 2021). The sugar amount per flower was derived from the volume and concentration of nectar. Flower odor (none, weak, or strong) was assessed in the field. We also sorted each plant species according to its life form (climber, epiphyte, herb, shrub, tree).

2.4 | Drivers of plant-bird pollination interactions.

First, we excluded all plants visited fewer than five times. Second, we generated two sets of matrices: one incorporating the robbing events and the other excluding them. We excluded those plants from the given sunbird diet where robbing events exceeded 50% of all visits. In some instances, the number of robbing events can be underestimated owing to difficulties in observing bird behavior. We built a matrix comprising all interactions recorded at all four sampling sites and during both seasons (hereafter "full matrix") for each of these matrix sets. Similarly, we built separate matrices for the interactions recorded in both seasons (hereafter, "season-based matrices").

We evaluated the importance of abundance, morphological matching, and nectar sugar content in explaining the observed interactions. We created interaction probability matrices and compared them to the observed interactions using a likelihood approach, following Vázquez et al. (2009). The observed interaction matrices (full and season-based) represented the total number of sunbird-plant interactions, with and without robbing events. For each observed matrix, we built probability matrices with exact dimensions based on the abundance, morphology, and nectar sugar content as follows:

Abundance (*Abu*): Multiplication of sunbird and plant abundance, representing a proxy for neutrality where interaction probabilities correlate with partner abundance.

Morphology (*Mor*): Cell entries represented morphological matching between interacting partners, taking only positive values. Each cell expressed the division of the tube and bill length. Values greater than one indicated longer flower tubes, whereas values smaller than one denoted shorter floral tubes. Values of one indicated perfect trait-matching.

Nectar sugar content (*Nec*): Cell entries denoted the amount of sugar per plant individual as a proxy for the reward offered by each plant species. In this matrix, each sunbird species had the same probability. Higher sugar content corresponded to higher probabilities.

We combined these three probabilistic matrices into all possible combinations to explore the various drivers of observed interactions. We also included a null model (Null) in which all species had the same interaction probability (Vázquez et al., 2009). Before conducting the likelihood analysis, we normalized the matrices to one for comparison. When multiple drivers were combined, the probabilistic matrices were re-normalized.

To compare the quality of the individual models, we calculated the difference in the *Akaike Information Criterion* (ΔAIC) between each model and the model with the lowest AIC. Note that the model with ΔAIC of 0 was considered the best. To account for model complexity, we used the number of species in each matrix as a parameter, whereas the null model had only one parameter (Vizentin-Bugoni et al., 2014).

All analyses were performed using the *stats* package in the R software (R Core Team, 2022), assuming a multinomial distribution.

2.5 | Seasonal β-diversity of interactions

We calculated interaction turnover in the whole network (βWN) to explore the seasonal changes in the networks for the season-based matrices. When interactions totally overlap across seasons, βWN is zero, whereas when no interactions are found from one season to another, βWN is one. We further explored the causes of interaction seasonal β-diversity between the seasons by calculating its two components. βST represents the contribution of species turnover to interaction turnover. βOS represents the contribution of interaction rewiring among the shared species. We used the "*betalinkr*" function from the *bipartite* R package (Dormann et al., 2008) to conduct these analyses.

2.6 | Testing the predictive power of bird traits for complex traits of visited flowers

We first calculated the sunbird-plant interaction frequencies at each study site as follows (Equation 1):

$$\textit{Visitation frequency} = \left(\frac{\textit{n}^\circ\ \textit{of visits}}{\textit{observed time}}\right) \times \textit{plant individuals per ha} \quad (1)$$

Thus, we obtained the interaction frequency that accounted for plant abundance at each study site. The mean of all the values was calculated if an interaction between the same species occurred across several sampling sites. Then, we built full and season-based matrices like those described above (Figure S1a).

To reveal the traits of visited plants by individual sunbird species, we calculated for each sunbird species a weighted mean of plant traits in each of the matrices explained above, as follows (Equation 2):

$$\textit{Weigthed plant trait of visited plants} = \frac{\sum_{i=1}^{n}\left(\textit{trait value}_i \times \textit{interaction frequency}_i\right)}{\sum_{i=1}^{n} \textit{interaction frequency}_i} \quad (2)$$

where a particular trait (e.g., tube length) of plant *i* was multiplied by the interaction frequency of a specific sunbird-plant interaction and divided by the sum of frequencies of all the interactions that bird had (hereafter "bird × trait of visited plant matrices", Figure S1a). All non-numerical variables (e.g., life form, flower position, symmetry) were dummy-coded into numerical variables, and the weighted mean of the visited floral traits was calculated similarly. The final matrices that entered the analyses had the structure of $n \times p$, where n represents the sunbird species, and p represents the weighted mean of the visited plant traits (Figure S1a).

Based on the length of gradients (i.e., 2.0 SD; Ter Braak & Šmilauer, 2012), Redundancy analysis (RDA) was chosen to test the predictive power of bird traits on the complex of visited plant traits on the full and seasonal bird × trait of visited plant trait matrices. All variables were centered and standardized. We tested the significance of each bird trait by using Monte Carlo tests with 999 permutations. The RDA analyses were conducted using CANOCO 5 software (Ter Braak & Šmilauer, 2012).

2.7 | Testing the segregation of functional feeding niches

To determine whether the feeding niches of the birds were segregated according to the plant traits they visited, we opted for an Euclidean distance approach. The individual observed interaction matrices from each sampled location were null modeled. 999 iterations were performed using the "*Vaznull*" function from the *bipartite* R package (Dormann et al., 2008; Figure S1b). Second, we combined each individual null matrix into a full, wet, or dry-season matrices. Then, we calculated the weighted plant trait matrix for each composed null matrix using the function "*cwm*" from the *BAT* R package (Cardoso et al., 2015). Next, we calculated an Euclidean distance matrix for each of these null bird × plant trait matrices, from which we obtained the mean Euclidean distance. We then calculated the Euclidean distance matrix and mean Euclidean distance for the observed full, wet, and dry-season matrices. We compared the observed Euclidean distances with the null models.

Additionally, we performed pairwise comparisons of the null distribution of Euclidean distances and compared them with the observed distribution for each sunbird species. Finally, we tested the significance of the observed values by comparing them with the null models (Figure S1b).

3 | RESULTS

In total, we recorded 39 plant species that interacted with 11 sunbird species (i.e., full matrices; Figure 1). The dry season had 28 plants and 10 sunbird species in both types of matrices (Figure 1). During the rainy season, when accounting for robbing events, the matrix comprised 20 plant species and five sunbird species. Nevertheless, when robbing was excluded, only four sunbird species interacted with 19 plant species.

We recorded 8364 and 7713 interactions, for the full matrices with and without robbing events, respectively. Plants that were commonly visited during the dry season included: *Anthonotha fragrans*, *Kigelia africana*, *Nuxia congesta*, and *Tabernaemontana ventricosa* (Table S3). All these plants were trees. During the wet season, *Impatiens niamniamensis*, *Thoningia sanguinea*, *Anthocleista scandens*, and *Psychotria hypsophila* were commonly visited, with these plants having various life forms (i.e., herb, liana, and shrub). In total, 651 robbing events were recorded. Frequently robbed plants included *Sabicea pilosa*, *Kigelia africana*, *Impatiens niamniamensis*, and *Acanthopale decempedalis*. *Cinnyris reichenowi* was often observed robbing (e.g., 78.6% of all visits to *Acanthopale decempedalis* flowering at Mann Spring wet season, Table S3).

3.1 | Drivers of plant-bird pollination interactions

The best descriptor for the full matrix, including robbing events, was the interaction between abundance, morphological matching, and sugar content in nectar (Figure 2). The dry-season matrix was best explained by the same model, with and without robbing events. However, the model that only considered the interaction between abundance and nectar performed almost as well as the complete interaction model. The model that included abundance and morphology best explained the interactions in the wet season matrices (Figure 2). We found the Null model to be the most parsimonious for the full matrix, excluding robbing events (Figure 2).

3.2 | Seasonal β-diversity of interactions

When excluding robbing events, the seasonal interaction turnover was 75.3% ($\beta WN = 0.753$), indicating a nearly complete turnover from season to season. This high interaction turnover was mainly explained by the high species turnover between the two seasons ($\beta ST = 0.728$; 96.68% of the total βWN; Table 1). Moreover, both seasonal matrices were highly dissimilar in terms of species composition ($\beta S = 0.639$). Interaction rewiring among shared species represented a small fraction of the variation in interactions between seasons ($\beta OS = 0.025$, Table 1). The season-based matrices with robbing events showed similar results (Table S4).

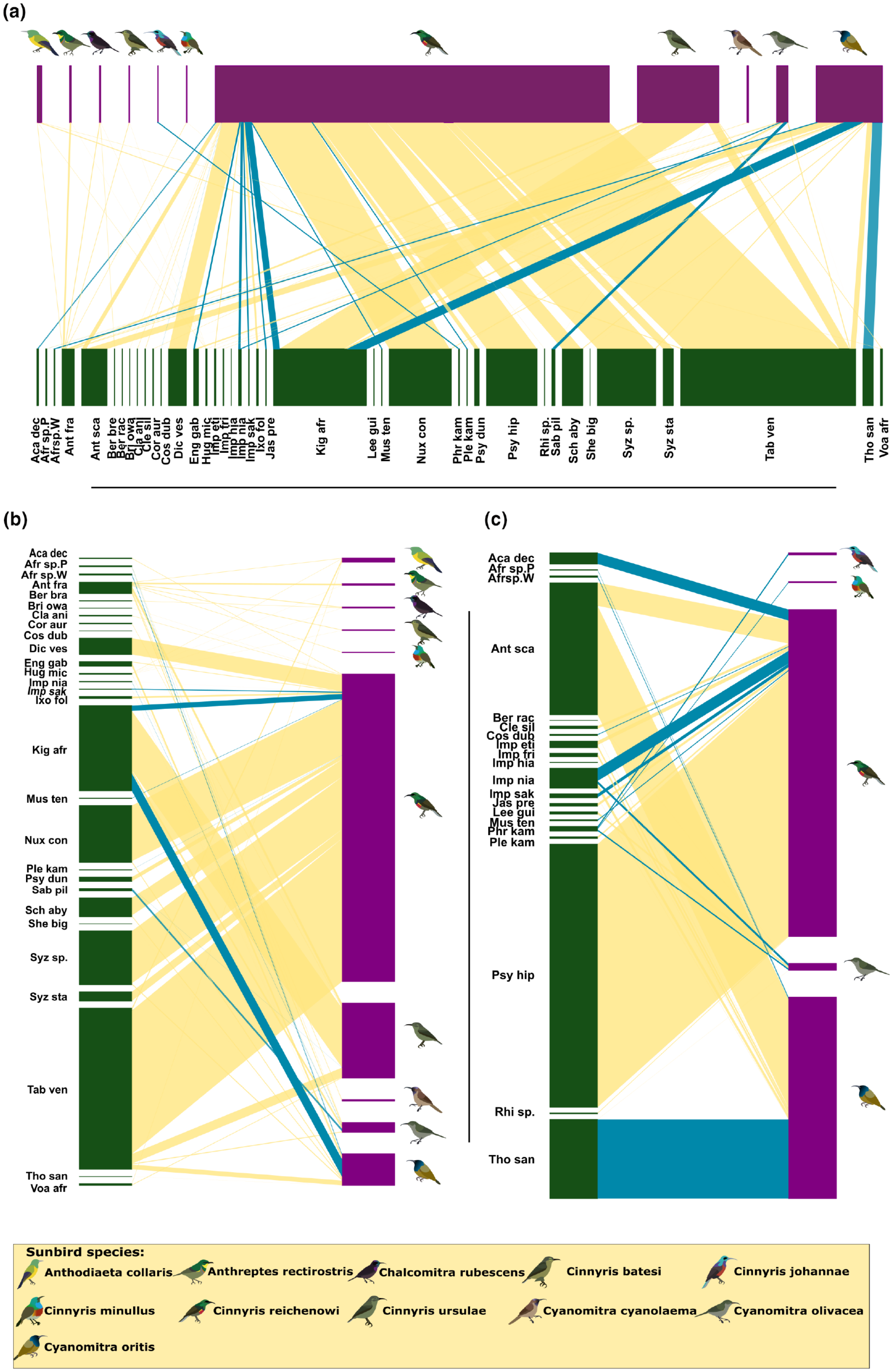
3.3 | Testing the predictive power of bird traits for complex traits of visited flowers

Bill length significantly structures the plant-bird interactions when excluding robbing events (Table 2). It was closely related to floral tube length, flowers in an upright position, and floral tube width (Figure 3). Nevertheless, none of the other tested bird traits showed a significant relationship with the plant traits (Table 2). The RDA performed for the full matrix, including the robbing events, found no significant relationship between plant and bird traits (Table S5). Analyses of individual seasonal matrices, with and without robbing, showed similar, but not significant, results (Table S6–S9).

Cyanomitra olivacea and *Cinnyris ursulae* visited plants with partially exposed, horizontal anthers and actinomorphic symmetry. *Cinnyris reichenowi and Cinnyris batesi* visited medium to large flowers with high nectar volume, pendant flowers, and herbaceous life forms. *Chalcomitra rubescens* and *Anthodiaeta collaris* visited plants with low nectar concentrations and weak odor. *Cinnyris minullus*, *Cyanomitra cyanolaema*, and *Anthreptes rectirostris* visited plants exhibiting flowers in all directions, featuring exposed anthers and zygomorphic symmetry. *Cyanomitra oritis* visited plants with long and wide floral tubes, whose flowers are upright and of shrub life forms. Finally, *Cinnyris johannae* visited shrubs with long and wide floral tubes.

3.4 | Testing the segregation of functional feeding niches

The observed mean Euclidean distance for all analyzed matrices was smaller than expected in a random scenario (Table 3 and Table S10). Therefore, all sunbird-visited plants were more similar than that anticipated by the null models. Diverse patterns emerged in plant functional niches among bird species pairs, encompassing segregation, overlap, and “no pattern” scenarios. In most cases, the observed Euclidean distance fell within the random distribution (i.e., no pattern scenario; Figures S2 and S3). In some instances, the observed Euclidean distance differed significantly from the random distribution. *Cinnyris reichenowi* visited plants with functional floral traits like six other sunbird species (Tables S11 and S12, Figure S2). Conversely, *Cyanomitra olivacea* showed the greatest dissimilarity in visited floral traits when accounting for the robbing events (Figure S2 and Table S11). *Cyanomitra olivacea* differed in its feeding niche from three sunbird species (i.e., *Anthodiaeta collaris*, *Anthreptes rectirostris*, and *Cyanomitra oritis*).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Tab ven
Tho san
Voa afr
(c)
Aca dec
Afr sp.P
Afrsp.W
Ant sca
Ber rac
Cle sil
Cos dub
Imp eti
Imp fri
Imp hia
Imp nia
Imp sak
Jas pre
Lee gui
Mus ten
Phr kam
Ple kam
Psy hip
Rhi sp.
Tho san
Sunbird species:
Anthodiaeta collaris
Anthreptes rectirostris
Chalcomitra rubescens
Cinnyris batesi
Cinnyris johannae
Cinnyris minullus
Cinnyris reichenowi
Cinnyris ursulae
Cyanomitra cyanolaema
Cyanomitra olivacea
Cyanomitra oritis

FIGURE 1 Bipartite networks of sunbird-plant interactions on Mt. Cameroon, robbing events included. (a) Full matrix; (b) Dry season; (c) Wet season. Plant species are represented by dark green boxes, whereas sunbird species are shown in purple. The frequency of each interaction is represented by the width of the lines (yellow and blue) joining the boxes. Dark blue lines represent the plant species in which robbing has been recorded. **PLANTS**: ***Aca dec***, *Acanthopale decempedalis*; **Afr sp.**, *Aframomum* sp. (two species); ***Ant sca***, *Anthocleista scandens*; ***Ant fra***, *Anthonotha fragans*; ***Berb ra***, *Berlinia bracteosa*; ***Berr ac***, *Bertiera racemosa*; ***Bri owa***, *Brillantasia owariensis*; ***Cla ani***, *Clausena anisata*; ***Cle syl***, *Clerodendrum sylvanum*; ***Cosd ub***, *Costus dubius*; ***Cora ur***, *Cordia aurantiaca*; ***Dic ves***, *Dicranolepis vestita*; ***Engg ab***, *Englerina gabonensis*; ***Hugm ic***, *Hugonia micans*; ***Imp eti***, *Impatiens etindensis*; ***Imp fri***, *Impatiens frithii*; ***Imp hia***, *Impatiens hians*; ***Imp nia***, *Impatiens niamniamensis*; ***Imp sak***, *Impatiens sakeriana*; ***Ixof ol***, *Ixora foliosa*; ***Jas pre***, *Jasminum preussii*; ***Kig afr***, *Kigelia africana*; ***Lee gui***, *Leea guineensis*; ***Mus ten***, *Mussaenda tenuiflora*; ***Nux con***, *Nuxia congesta*; ***Phr kam***, *Phragmantera kamerunensis*; ***Ple kam***, *Plectranthus kamerunensis*; ***Psyd un***, *Psydrax dunalpii*; ***Psy hip***, *Psychotria hypsophila*; ***Rhi* sp.**, *Rhipidoglossum* sp.; ***Sab pil***, *Sabicea pilosa*; ***Scha by***, *Schefflera abyssinica*; ***She big***, *Sherbournia bignoniflora*; ***Syz* sp.**, *Syzygium* sp.; ***Syz sta***, *Syzygium staudtii*; ***Tab ven***, *Tabernaemontana ventricosa*; ***Thos an***, *Thoningia sanguinea*; ***Voa afr***, *Voacanga africana*.

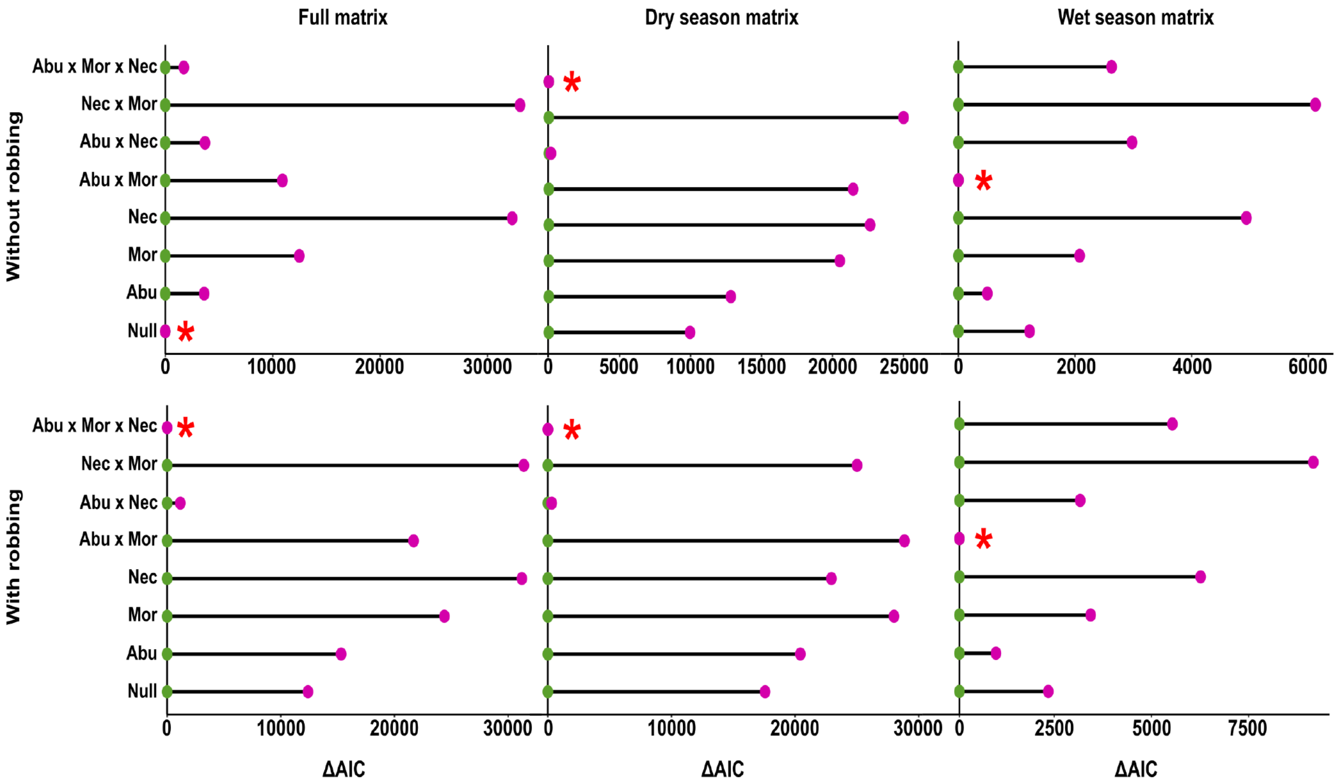

FIGURE 2 ΔAIC values of probability matrices evaluated to explain the observed sunbird-plant interactions in Mount Cameroon. Probability matrices: abundance (*Abu*), morphological matching (*Mor*), nectar sugar content per plant (*Nec*), and their respective combinations. Red asterisks represent the most parsimonious model in each of the analyzed matrices.

During the dry season, *Cyanomitra olivacea* acted as a true specialist, visiting plants with traits different from those of most other species (Figures S4 and S5, and Tables S13 and S14). This situation occurred with and without robbing events. During the wet season, *Cyanomitra olivacea* and *Cyanomitra oritis* visited plants with similar characteristics when robbing events were excluded (Figure S6, Table S15). Also, the visited plants by *Cinnyris reichenowi*, *Cinnyris johannae*, and *Cyanomitra oritis* were different than expected in a random scenario when excluding the robbing events.

4 | DISCUSSION

Our study confirms that sunbird-plant interactions are driven by both mechanisms evaluated. These findings partially align with our initial hypothesis and with earlier research. Previous studies have found that the observed interactions are caused by morphology (Bergamo et al., 2017; Maglianesi et al., 2015; Maruyama et al., 2014; Vizentin-bugoni et al., 2014) or abundance (Sazatormil et al., 2016; Vázquez et al., 2009). In our system, the dry-season matrices were explained by the interaction between abundance, morphology, and nectar. The model that solely considered the interplay between abundance and nectar nearly equally accounted for the interactions observed during this season. Among bird traits, only bill length correlated with the complex of visited plant traits, agreeing with other studies (Maglianesi et al., 2015). Morphological matching is more important during the wet season because of the phenological patterns of our study system. Contrary to our hypothesis, bird-feeding niches determined by plant traits overlap more than in a random scenario.

4.1 | Drivers of sunbird-plant interactions

The interaction between abundance, morphology, and nectar best explained the dry-season matrices. However, the model without morphological variables was not significantly worse (Figure 2). Sunbirds frequently interacted with non-ornithophilous plants during this season (e.g., *Anthonotha fragrans* and *Nuxia congesta*). Despite low nectar volumes per flower, these plants, which flowered massively, attracted all non-specialist sunbird species (Figure 3), providing a large nectar reservoir. Chmel et al. (2021) demonstrated that the frequency of sunbird-plant interactions was determined by nectar reward per plant rather than other floral traits, regardless of pollination syndrome. Nectar availability also influenced sunbird population size, showing a linear increase with increasing nectar availability (Schmid et al., 2016). Hummingbirds also visited plants with greater nectar rewards more frequently (Fenster et al., 2006). Moreover, Janeček et al. (2021) found that ornithophilous flowers produced higher amounts of sugar. In this scenario, sunbirds could choose between two options. 1/ Actively select ornithophilous flowers that produce suitable amounts of sugar-rich nectar, as more specialized sunbird species; 2/ Feed on less rewarding flowers, massively flowering nearby, as most sunbird species in this study. While these plants produce less sugar per flower, they ultimately provide more energy to birds because of the lower cost of foraging.

TABLE 1 β-diversity of interactions for the season-based matrices without robbing. Interaction turnover (β_{WN}) was split into two components: species turnover (β_{ST}) and interaction rewiring (β_{OS}). Furthermore, β_{ST} was partitioned into the effects of the lower ($\beta_{ST\ low}$), higher ($\beta_{ST\ high}$) or both levels ($\beta_{ST\ lh}$) of the bipartite networks. The effects of species replacement ($\beta_{WN\ rep}/\beta_{OS\ rep}$) and species richness ($\beta_{WN\ rich}/\beta_{OS\ rich}$) on β_{WN} and β_{OS} are also shown.

Seasonal β-diversity of interactions				
β_{WN}	0.753	$\beta_{WN\ rep}$ 0.395	$\beta_{WN\ rich}$ 0.358	
β_{ST}	0.639	$\beta_{ST\ low}$ 0.469	$\beta_{ST\ high}$ 0.000	$\beta_{ST\ lh}$ 0.259
β_{OS}	0.025	$\beta_{OS\ rep}$ 0.000	$\beta_{OS\ rich}$ 0.025	

Conversely, the wet season matrices were best explained by the interaction between abundance and morphology (Figure 2). Based on their abundance, birds will still seek plants that offer them the greatest energetic reward at a minimal energy cost. However, ornithophilous plants make morphological trait matching more important during this season. Thus, there is a continuum between visiting the most abundant plants and those that produce suitable amounts of sucrose-rich nectar, similar to what was suggested by Gravel et al. (2006).

4.2 | Seasonal β-diversity of interactions

A high seasonal interaction turnover of sunbird-plant interactions was recorded (βWN = 0.753), primarily driven by species turnover, consistent with findings in other plant-pollinator interaction studies (Chacoff et al., 2018; Olesen et al., 2011). This species turnover underscores the seasonal dynamism of the studied ecosystem (Figure 1b,c). Thus, seasonal changes in resource availability may

TABLE 2 Forward selection analysis for the full matrix without robbing.

(a) Summary of the redundancy analysis results

Total variation	**% contribution of explanatory variables**	**Adj. Method**	**Adj. % explained variation**	
231.00	51.49	FDR	19.16	
Eigenvalue decomposition				
Axis	1	2	3	4
Value	0.3142	0.1496	0.0400	0.0111
Cumulative variation	31.42	46.39	50.39	51.49
P-canonical correlation	0.9470	0.7221	0.7611	0.3127
Explained fitted variation	61.03	90.08	97.85	100.00

(b) Variables tested

Trait	**Explained variability**	**% Contribution**	**Pseudo-F**	***p*-Value**	***p*-Value adj.**
Bill length	25.7	49.9	3.1	.005	.020*
Weight	9.7	18.8	1.2	.321	.641
Width	9.5	18.8	1.2	.306	.428
Depth	6.6	12.9	0.8	.614	.614

Note: (a) Summary of the results from the redundancy analysis (RDA); (b) bird traits tested: length of the bill, bird weight, and width and depth of the bill. Their significance was tested with 999 Monte Carlo permutations. Significant results are marked with asterisk.

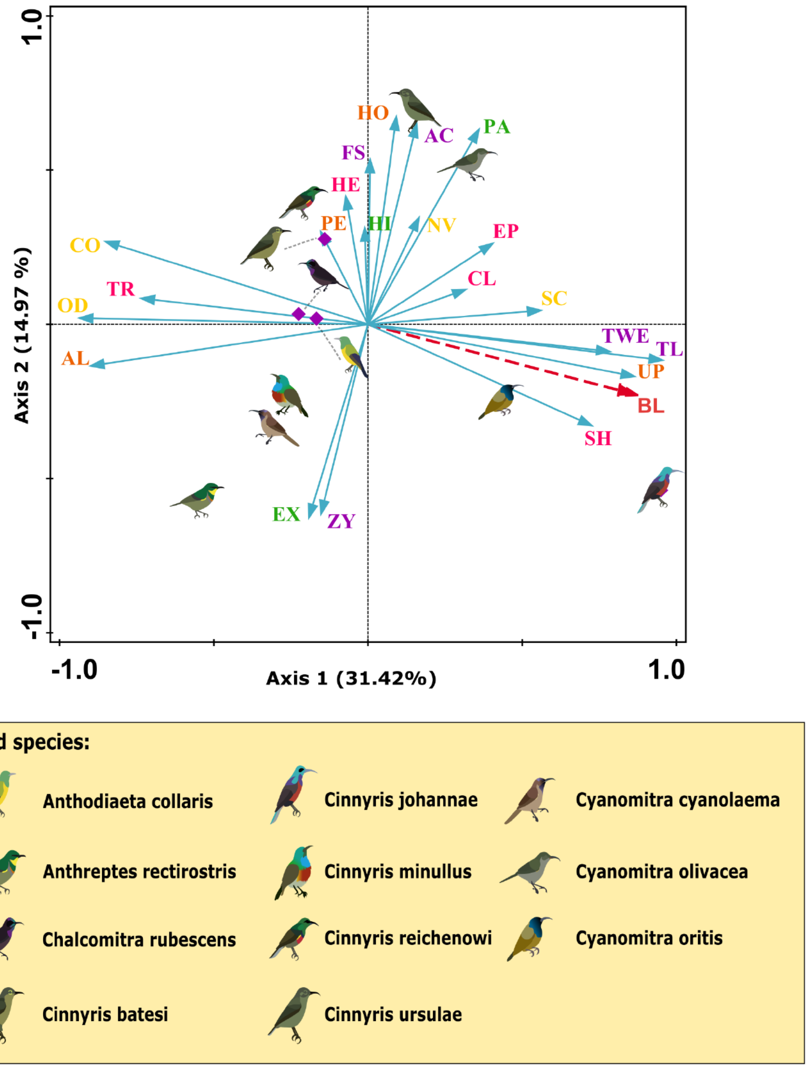

FIGURE 3 RDA triplot showing the relationship between bird and floral traits, as well as the relative position of each bird species within the morphospace, for the full matrix without robbing. The percentage of variability explained by each axis is shown in parentheses. For clarity, only significant bird traits are shown (red dashed arrow): bill length (BL). Five sets of floral traits were tested (blue solid arrows). Morphological floral traits (purple): corolla final size (FS), tube length (TL), and flower symmetry (AC and ZY). Pollinator attraction traits (yellow): nectar concentration (CO), and volume (NV), and odor of the flowers (OD). Anther position (green): exposed (EX), partially exposed (PA), hidden (HI). Flower position (orange): pendant (PE), horizontal (HO), upright (UP), all (AL). Life form (in pink): epiphyte (EP), climber (CL), herb (HE), shrub (SH), and tree (TR).

TABLE 3 Results from the modeling of bird-feeding niches (excluding robbing events) and its comparison with the observed values.

Modeling of bird-feeding niches			
Matrix	**Obs. Dist.**	**N. Dist.**	***p*-Value**
Full	5.449	6.081	<.05
Wet	4.793	6.369	<.05
Dry	5.350	6.044	<.05

Note: Mean observed Euclidean distance (Obs. Dist.) and null modeled mean Euclidean distance (N. Dist.) for all the matrices analyzed.

provoke local sunbird migration, potentially explaining the lower number of sunbird species observed during the wet season.

4.3 | Effects of seasonality

Morphological matching is seasonally dependent. The dry-season interactions were nearly equally explained by the model that only included abundance and nectar. These results support the hypothesis that trait matching is more significant in the wet season. Moreover, the high species turnover between the two seasons supports this idea. Nevertheless, our findings may be influenced by the limited number of sunbird species found during the wet season, which tend to have specialized adaptations for nectarivory. However, as indicated by previous studies (Huang et al., 2017), birds are more efficient pollinators in challenging and cold climates, prompting plants to depend on them for pollination services. Additionally, we found more ornithophilous plants during the rainy season on Mt. Cameroon (e.g., *Impatiens frithii*; *Englerina gabonensis*). Hence, specific flower shapes that favor bird pollination are more common during the rainy season as an adaptation to heavy rainfall (Pacini & Nepi, 2007). Klomberg et al. (2022) reported more closed flowers during the rainy season on Mt. Cameroon. This evidence suggests that ornithophilous plant phenology and challenging environmental conditions promote trait-matching (Maruyama et al., 2014). Thus, the rainy season likely exerts strong selective pressure on interacting partners to have well-attuned traits.

4.4 | Relationship between bird and plant traits and the effects of robbing

Only bill length predicted the complexity of the visited plant traits. It correlates with tube length and width and flowers in an upright position (Figure 3). Our results were like those of Izquierdo-Palma et al. (2021). Flowers visited by *Phaetornis longirostris* had an average corolla length that was practically identical to the average bill length of the birds. Thus, the correlation between flower position and dimensions (i.e., length and width) with bill length enables sunbirds to exploit their resources more efficiently (Pyke, 2016), and plants to secure pollination services. Nonetheless, our results may be driven by long-billed sunbirds interacting with long-tubed plant species. These species are specialized community members and therefore exert stronger selective pressure for this relationship to occur (Fenster, 1991).

When robbing events were included, none of the bird attributes explained the complexity of visited plant traits. Flower morphology influences how pollinators extract and gain access to floral rewards. Short-billed sunbirds robbed from long-tube flowers (e.g., Janeček et al., 2015; Padyšáková et al., 2013). Therefore, robbing is expected to be minimized in perfect trait-matching. However, we also observed sunbirds robbing ornithophilous plants (e.g., *Cyanomitra olivacea* on *Impatiens niamniamensis*). Also, Sakhalkar et al. (2023) demonstrated that sunbirds frequently rob ornithophilous plants. Even a single visiting species can pollinate and rob during distinct visits to a plant species. These findings indicate that better trait-matching does not guarantee avoidance of robbing and that trait-mismatching affects how sunbirds access nectar.

4.5 | Overlap of bird-feeding niches

Despite bill length predicted the complex of visited plants, bird-feeding niches overlapped more than in a random scenario. All sunbird species congregated around the short-tubed flowers (Figure S7). Long-billed sunbirds visited both short and long-tubed flowers, masking niche segregation based on plant traits. An exception was *Cinnyris johannae*, which exclusively visited a plant species with a 75-mm long tube (*Phragmanthera kamerunensis*).

During the dry season, *Anthonotha fragrans* attracted most sunbirds at low elevations (Figure 1b), whereas *Impatiens niamniamensis* acted as another hub for sunbird species during the wet season (Figure 1c), obscuring niche segregation. In situations of low resource availability, previous studies found that long-billed hummingbirds exhibit greater specialization (Tinoco et al., 2017), with competition constraining their niche expansion and reducing overlap. Contrarily, our study revealed that *Cyanomitra olivacea* exhibited greater niche segregation when resource availability was highest (i.e., dry season). This supports findings from other mutualistic networks, such as seed dispersal and pollination, where species tend to constrain feeding niches at high resource availability (Albrecht et al., 2013; Fontaine et al., 2008). Therefore, *Cyanomitra olivacea* selectively foraged on the plant species with the largest amount of nectar. Similarly, Janeček et al. (2022) found that sunbirds were more specialized at lower elevations where *Cyanomitra olivacea* is found. However, at high elevations, the networks were more generalized, which aligns with our findings regarding *Cinnyris reichenowi*. This species displayed a generalist feeding strategy and shared its feeding niche with most other species.

5 | CONCLUSIONS

Our study, like Vizentin-Bugoni et al. (2018), highlights the influence of neutral and niche-based processes on sunbird-plant interactions. In our study, morphological trait-matching was crucial in specialized interactions between ornithophilous plants and specialized sunbird species, especially during the wet season when specialized plants bloom. However, neutral processes and nectar rewards are important during the dry season when sunbirds interact with plants that flower massively and convey a huge amount of nectar. Thus, in this scenario, the wet season exerts stronger selective pressure on the traits of both partners to be more attuned. A good example is the long-billed sunbird *Cinnyris johannae*, which only interacts with the long-tubed *Phragmanthera kamerunensis*. Nonetheless, we did not observe niche segregation among the sunbird species. Further research is needed to understand the observed pattern of niche overlap, as the absence of competition likely influences it.

AUTHOR CONTRIBUTIONS

GUG and ŠJ formulated ideas. GUG, KC, PJ, JM, YK, FLE, LLM, MMN, RT, and ŠJ conducted fieldwork. KC and PJ analyzed the video material. GUG performed statistical analyses and led the manuscript writing. All authors contributed critically to the drafts and approved the manuscript for publication.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be available in the Zenodo repository at https://doi.org/10.5281/zenodo.10181316.

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REFERENCES

Albrecht, J., Berens, D. G., Blüthgen, N., Jaroszewicz, B., Selva, N., & Farwig, N. (2013). Logging and forest edges reduce redundancy in plant-frugivore networks in an old-growth European forest. *Journal of Ecology*, *101*, 990–999. https://doi.org/10.1111/1365-2745.12105

Bartoš, M., Janeček, Š., Padyšaková, E., Patáčová, E., Altman, J., Pešata, M., & Kantorová & Tropek, R. (2012). Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: A comparison with six other co-flowering species. *South African Journal of Botany*, *78*, 63–74. https://doi.org/10.1016/j.sajb.2011.05.015

Bergamo, P. J., Wolowski, M., Maruyama, P. K., Vizentin-Bugoni, J., Carvalheiro, L. G., & Sazima, M. (2017). The potential indirect effects among plants via shared hummingbird pollinators are structured by phenotypic similarity. *Ecology*, *98*, 1849–1858. https://doi.org/10.1002/ecy.1859

Biddick, M., & Burns, K. C. (2018). Phenotypic trait matching predicts the topology of an insular plant–bird pollination network. *Integrative Zoology*, *13*, 339–347. https://doi.org/10.1111/1749-4877.12319

Brown, J. H., Calder, W. A., III, & Kodric-brown, A. (1978). Correlates and consequences of body-size in nectar feeding birds. *American Zoologist*, *18*, 687–700.

Butler, H. C., Cozien, R. J., & Johnson, S. D. (2022). For the birds? Constrasting pollination and breeding systems of the paintbrush lilies *Scadoxus puniceus* and *S. Membranaceus* (*Amaryllidaceae*). *Plant Systematics and Evolution*, *308*, 6. https://doi.org/10.1007/s00606-021-01798-5

Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT—biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods in Ecology and Evolution*, *6*, 232–236. https://doi.org/10.1111/2041-210X.12310

Chacoff, N. P., Resasco, J., & Vázquez, D. P. (2018). Interaction frequency, network position, and the temporal persistence of interactions in a plant-pollinator network. *Ecology*, *99*(1), 21–28. https://doi.org/10.1002/ecy.2063 Epub 2017.

Chmel, K., Ewome, F. L., Uceda-Gómez, G., Klomberg, Y., Mertens, J. E. J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective. *Oikos*, *130*, 1411–1424. https://doi.org/10.1111/oik.08052

Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and molecular context. *Journal of Experimental Botany*, *59*, 715–727. https://doi.org/10.1093/jxb/ern009

Dormann, C. F., Gruber, B., & Frund, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, *8*, 8–11.

Dupont, Y. L., Hansen, D. M., & Olesen, J. M. (2003). Structure of a plant-flower-visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography*, *26*, 301–310.

Faegri, K., & van der Pijl, L. (1979). *The principles of pollination ecology*. Pergamon Press.

Fenster, C. B. (1991). Selection on floral morphology by hummingbirds. *Biotropica*, *23*, 98–101. https://doi.org/10.2307/2388696

Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination syndromes and floral specialization. *Annual Review of Ecology Evolution and Systematics*, *35*, 375–403.

Fenster, C. B., Cheely, G., Dudash, M. R., & Reynolds, R. J. (2006). Nectar reward and advertisement in hummingbird-pollinated *Silene virignica* (Caryophyllaceae). *American Journal of Bonaty*, *93*, 1800–1807. https://doi.org/10.3732/ajb.93.12.1800

Fenster, C. B., Reynolds, R. J., Williams, C. W., Makowsky, R., & Dudash, M. R. (2015). Quantifying hummingbird preference for floral trait combinations: The role of selection on trait interactions in the evolution of pollination syndromes. *Evolution*, *69*, 1113–1127. https://doi.org/10.1111/evo.12639

Fontaine, C., Collin, C. L., & Dajor, I. (2008). Generalist foraging of pollinators: Diet expansion at high density. *Journal of Ecology*, *96*, 1002–1010.

Geerts, S., & Pauw, A. (2009). Hyper-specialization for long-billed bird pollination in a guild of South African plants: The Malachite Sunbird pollination syndrome. *South African Journal of Botany.*, *75*, 699–706. https://doi.org/10.1016/j.sajb.2009.08.001

Gravel, D., Canham, C. D., Beaudet, M., & Messier, C. (2006). Reconciling niche and neutrality: The continuum hypothesis. *Ecology Letters*, *9*(4), 399–409. https://doi.org/10.1111/j.1461-0248.2006.00884.x

Hargreaves, A. L., Langston, G. T., & Johnson, S. D. (2019). Narrow entrance of short-tubed Aloe flowers facilitates pollen transfer on long sunbird bills. *South African Journal of Botany*, *124*, 23–28. https://doi.org/10.1016/j.sajb.2019.04.013

Hořák, D., & Janeček, Š. (2021). A geographical perspective on the relationship between Impatiens spur lengths and bill lengths of sunbirds in Afrotropical mountains. *Ecology and Evolution*, *11*, 3120–3129. https://doi.org/10.1002/ece3.7258

Huang, Z. H., Song, Y. P., & Huang, S. Q. (2017). Evidence for passerine bird pollination in Rhododendron species. *AoB Plants*, *9*, 1–10. https://doi.org/10.1093/aobpla/plx062

Hubbell, S. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography (MPB-32)*. Princeton University Press. https://doi.org/10.1515/9781400837526

Inouye, D. W. (1983). The ecology of nectar robbing. In B. Beattey & T. Elias (Eds.), *The biology of Nectaries*, ed (pp. 153–173). Columbia University Press.

Irwin, R. E., & Brody, A. K. (1998). Nectar robbing in ipomopsis aggregata: Effects on pollinator behavior and plant fitness. *Oecologia*, *116*, 519–527. https://doi.org/10.1007/s004420050617

Irwin, R. E., Brody, A. K., & Waser, N. M. (2001). The impact of floral larceny on individuals, populations, and communities. *Oecologia*, *129*, 161–168. https://doi.org/10.1007/S004420100739

Izquierdo-Palma, J., Arizmendi, M. C., Lara, C., & Ornelas, J. F. (2021). Forbidden links, trait matching and modularity in plant-hummingbird networks: Are specialized modules characterized by higher phenotypic floral integration? *PeerJ*, *9*, e10974. https://doi.org/10.7717/peerj.10974

Janeček, Š., Bartoš, M., & Njabo, K. Y. (2015). Convergent evolution of sunbird pollination systems of Impatiens species in tropical Africa and hummingbird systems of the New World. *Biological Journal of the Linnean Society*, *115*, 127–133. https://doi.org/10.1111/bij.12475

Janeček, Š., Chmel, K., Ewome, F. L., Hrubá, K., Klomberg, Y., Kobe, I. N., Kouede, R. D., Mertens, J. E. J., Njie, M. M., & Tropek, R. (2021). Differences in nectar traits between ornithophilous and entomophilous plants on mount Cameroon. *Plants*, *10*(6), 1161. https://doi.org/10.3390/plants10061161

Janeček, Š., Chmel, K., Mlíkovský, J., Uceda-Gomez, G., Janečková, P., Fominks, N. T., Njie, M. M., & Ewome, F. L. (2022). Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. *Oecologia*, *199*, 885–896. https://doi.org/10.1007/s00442-022-05234-4

Janeček, Š., Chmel, K., Uceda-Gómez, G., Janečková, P., Chmelová, E., Sejfová, Z., & Ewome, F. L. (2020). Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution*, *10*, 1784–1793. https://doi.org/10.1002/ece3.5942

Janeček, Š., Riegert, J., Sedláček, O., Bartoš, M., Hořák, D., Reif, J., Padyšáková, E., Fainová, D., Antczak, M., Pešata, M., Mikeš, V., Patáčová, E., Altman, J., Kantorová, J., Hrázský, Z., Brom, J., &

Doležal, J. (2012). Food selection by avian floral visitors: An important aspect of plant-flower visitor interactions in West Africa. *Biological Journal of Linnean Society*, *107*, 355–367. https://doi.org/10.1111/j.1095-8312.2012.01943.x

Janečková, P., Sejfová, Z., Janeček, Š., Chmel, K., Chmelová, E., & Ewome, F. L. (2020). Behavioural correlates of drinking speed in two West African sunbird species. *Bird Study*, *67*, 540–542. https://doi.org/10.1080/00063657.2021.1917510

Johnson, S. D., Kiepiel, I., & Robertson, A. W. (2020). Functional consequences of flower curvature, orientation and perch position for nectar feeding by sunbirds. *Biological Journal of Linnean. Society*, *131*, 822–834. https://doi.org/10.1093/biolinnean/blaa154

Johnson, S. D., & Nicolson, S. W. (2008). Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biology Letters*, *4*, 49–52. https://doi.org/10.1098/rsbl.2007.0496

Klomberg, Y., Tropek, R., Mertens, J. E. J., Kobe, I. N., Hodeček, J., Raška, J., Fominka, N. T., Souto-Vilarós, D., Janečková, P., & Janeček, Š. (2022). Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. *Ecology Letters*, *25*, 839–850. https://doi.org/10.1111/ele.13958

Küpper, W., Sommer, J. H., Lovett, J. C., Mutke, J., Linder, H. P., Beentje, H. J., van Rompaey, R. S. A. R., Chatelain, C., Sosef, M., & Barthlott, W. (2004). Africa's hotspots of biodiversity redefined. *Annals of the Missouri Botanical Garden*, *91*, 525–535.

Maglianesi, M. A., BlüThgen, N., BöHning-Gaese, K., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, *95*, 3325–3334. https://doi.org/10.1890/13-2261.1

Maglianesi, M. A., Böhning-Gaese, K., & Schleuning, M. (2015). Different foraging preferences of hummingbirds on artificial and natural flowers reveal mechanisms structuring plant–pollinator interactions. *Journal Animal Ecology*, *84*, 655–664. https://doi.org/10.1111/1365-2656.12319

Maicher, V., Sáfián, S., Murkwe, M., Przybyłowicz, Ł., Janeček, Š., Fokam, E. B., Pyrcz, T., & Tropek, R. (2018). Flying between raindrops: Strong seasonal turnover of severalLepidoptera groups in lowland rainforests of Mount Cameroon. *Ecology and Evolution*, *8*(24), 12761–12772. https://doi.org/10.1002/ece3.4704

Maicher, V., Sáfián, S., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., Kobe, I. N., Janeček, Š., Mertens, J. E. J., Fokam, E. B., Pyrcz, T., Doležal, J., Altman, J., Hořák, D., Fiedler, K., & Tropek, R. (2020). Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *Journal of Biogeography*, *47*, 342–354. https://doi.org/10.1111/jbi.13740

Maruyama, P. K., Vizentin-Bugoni, J., Oliveira, G. M., Oliveira, P. E., & Dalsgaard, B. (2014). Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. *Biotropica*, *46*, 740–747.

Navarro, L. (2000). Pollination ecology of *Anthyllis vulneraria* subsp. *Vulgaris* (Fabaceae): Nectar robbers as pollinators. *American Journal of Botany*, *87*, 980–985. https://doi.org/10.2307/2656997

Navarro, L., & Medel, R. (2009). Relationship between floral tube length and nectar robbing in Duranta erecta L. (Verbenaceae). *Biological Journal of Linnean Society*, *96*, 392–398. https://doi.org/10.1111/j.1095-8312.2008.01146.x

Nsor, C. A., Godsoe, W., & Chapman, H. M. (2019). Promiscous pollinators—Evidence from an Afromontane sunbird–plant pollen transport network. *Biotropica*, *51*, 538–548. https://doi.org/10.1111/btp.12669

Olesen, J. M., Bascompte, J., Dupont, Y. L., Elberling, H., Rasmussen, C., & Jordano, P. (2011). Missing and forbidden links in mutualistic networks. *Proceedings of the Royal Society B*, *278*, 725–732. https://doi.org/10.1098/rspb.2010.1371

Ollerton, J., Johnson, S. D., Cranmer, L., & Kellie, S. (2003). The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of Botany*, *92*, 807–834. https://doi.org/10.1093/aob/mcg206

Pacini, E., & Nepi, M. (2007). Nectar production and presentation. In S. W. Nicolson, M. Nepi, & E. Pacini (Eds.), (Eds.) *Nectaries and nectar* (pp. 167–214). Springer.

Padyšáková, E., Bartoš, M., Tropek, R., & Janeček, Š. (2013). Generalization versus specialization in pollination systems: Visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae). *PlosOne*, *8*, 1–8. https://doi.org/10.1371/journal.pone.0059299

Padyšáková, E., & Janeček, Š. (2016). Sunbird hovering behavior is determined by both the forager and resource plant. *Biotropica*, *48*, 687–693. https://doi.org/10.1111/btp.12345

Partida-Lara, R., Enríquez, P. L., Vázquez-Pérez, J. R., de Bonilla, E. P. D., Martínez-Ico, M., & Rangel-Salazar, J. L. (2018). Pollination syndromes and interaction networks in hummingbird assemblages in El Triunfo Biosphere Reserve, Chiapas, Mexico. *Journal of Tropical Ecology*, *34*, 293–307. https://doi.org/10.1017/S0266467418000263

Payne, S. L., Witkowski, E. T. F., & Symes, C. T. (2022). Specialist and generalist avian nectarivores co-dominate visitation to a summer-flowering grassland aloe. *South African Journal of Botany*, *144*, 284–294. https://doi.org/10.1016/j.sajb.2021.08.005

Pyke, G. H. (2016). Plant-pollinator co-evolution: It's time to reconnect with Optimal Foraging Theory and Evolutionarily Stable Strategies. *Perspectives in Plant Ecology Evolution and Systematics*, *19*, 70–76. https://doi.org/10.1016/j.ppees.2016.02.004

Ralph, C. J., Droege, S., & Sauer, J. R. (1995). Managing and monitoring birds using point counts: standards and applications. In C. J. Ralph, J. R. Sauer, & S. Droege (Eds.), *Monitoring bird populations by point counts*. Gen. Tech. Rep. PSW-GTR-149. (Vol. *149*, pp. 161–168). US Department of Agriculture, Forest Service, Pacific Southwest Research Station.

R Core Team. (2022). R: *A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rojas-Nossa, S. V., Sanchez, J. M., & Navarro, L. (2021). Nectar robbing and plant reproduction: An interplay of positive and negative effects. *Oikos*, *130*, 601–608. https://doi.org/10.1111/oik.07556

Sakhalkar, S. P., Janeček, Š., Klomberg, Y., Mertens, J. E. J., Hodeček, J., & Tropek, R. (2023). Cheaters among pollinators: Floral traits drive spatiotemporal variation in nectar robbing and thieving in Afrotropical rainforests. *Ecosphere*, *14*, 2022. https://doi.org/10.1101/2022.05.16.492032

Santamaria, L., & Rodríguez-Girones, M. A. (2014). Linkage rules for plant-pollinator networks: Trait complementarity or exploitation barriers. *Plos Biology*, *5*, 1–36. https://doi.org/10.1371/journal.pbio.0050031

Sazatormil, F. D., Moré, M., Benitez-Vieyra, S., Cocucci, A. A., Kitching, I. J., Schlumpberger, B. O., Oliverira, P. E., Sazima, M., & Amorim, F. W. (2016). Beyond neutral and forbidden links: morphological matches and the assembly of mutualistic hawkmoth-plant networks. *Journal of Animal Ecology*, *85*, 1586–1594. https://doi.org/10.1111/1365-2656.12509

Schmid, B., Notterbrock, H., Esler, K. J., Pagel, J., Pauw, A., Böhning-Gaese, K., Schurr, F. M., & Schleuning, M. (2016). Responses of nectar-feeding birds to floral resources at multiple spatial scales. *Ecography*, *39*, 619–629. https://doi.org/10.1111/ecog.01621

Sejfová, Z., Mlíkovský, J., Ewome, F. L., Janečková, P., Klomberg, Y., Njie, M. M., & Janeček, Š. (2021). Sunbirds' tendency to hover: The roles of energetic rewards, inflorescence architecture and rain. *Journal of Avian Biology*, *52*, 1–10. https://doi.org/10.1111/jav.02818

Snow, B. K., & Snow, D. W. (1972). Feeding niches of hummingbirds in a Trinidad Valley. *Animal Ecology*, *41*, 471–485. https://doi.org/10.2307/3481

Sonne, J., Zanata, T. B., Martín González, A. M., Cumbicus Torres, N. L., Fjeldså, J., Colwell, R. K., Tinoco, B. A., Rahbek, C., & Dalsgaard, B. (2019). The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. *Biotropica*, *51*, 205–218. https://doi.org/10.1111/btp.12637

Stang, M., Klinkhamer, P. G. L., & van der Meijden, E. (2007). Asymmetric specialization and extinction risk in plant-flower visitor webs: A matter of morphology or abundance? *Oecologia*, *151*, 442–453. https://doi.org/10.1007/s00442-006-0585-y

Temeles, E. J., Koulouris, C. R., Sander, S. E., & Kress, W. J. (2009). Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird. *Ecology*, *90*, 1147–1161. https://doi.org/10.1890/08-0695.1

ter Braak, C. J. F., & Šmilauer, P. (2012). *Canoco reference manual and user's guide: Software for ordination, version 5.0. Microcomputer Power.*

Tinoco, B. A., Graham, C. H., Aguilar, J. M., & Schleuning, M. (2017). Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. *Oikos*, *126*, 52–60. https://doi.org/10.1111/oik.02998

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022a). *AVONET: Morphological, ecological and geographical data for all birds. Figshare.* https://doi.org/10.6084/m9.figshare.16586228.v7

Tobias, J. A., Sheard, C., Pigot, A. L., Devenish, A. J. M., Yang, J., Sayol, F., Neate-Clegg, M. H. C., Alioravainen, N., Weeks, T. L., Barber, R. A., Walkden, P. A., MacGregor, H. E. A., Jones, S. E. I., Vincent, C., Phillips, A. G., Marples, N. M., Montaño-Centellas, F. A., Leandro-Silva, V., Claramunt, S., … Schleuning, M. (2022b). AVONET: Morphological, ecological and geographical data for all birds. *Ecology Letters*, *25*, 581–597. https://doi.org/10.1111/ele.13898

Tropek, R., Bartoš, M., Padyšáková, E., & Janeček, Š. (2013). Intenference competition between sunbirds and carpenter bees for the nectar of *Hypoestes aristata*. *African Zoology*, *48*, 392–394. https://doi.org/10.3377/004.048.0222

van der Pijl, L. (1961). Ecological aspects of flower evolution. *Evolution*, *15*, 44–59. https://doi.org/10.2307/2405990

Vázquez, D. P., Chacoff, N. P., & Cagnolo, L. (2009). Evaluating multiple determinants of the structure of plant-animal mutualistic networks. *Ecology*, *90*, 2039–2046. https://doi.org/10.1890/08-1837.1

Vizentin-Bugoni, J., Maruyama, P. K., de Souza, C. S., Ollerton, J., Rech, A. R., & Sazima, M. (2018). Plant-pollinator netwroks in the tropics: A review. In W. Dáttilo & V. Rico-Gray (Eds.), (eds) *Ecological networks in the tropics*. Springer. https://doi.org/10.1007/978-3-319-68228-0_6

Vizentin-Bugoni, J., Maruyama, P. K., & Sazima, M. (2014). Processes entangling interactions in communities: Forbidden links are more important than abundance in a hummingbird-plant network. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132397. https://doi.org/10.1098/rspb.2013.2397

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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SUPPORTING INFORMATION CHAPTER I

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Drivers of sunbird-plant interactions in Mt. Cameroon: between neutrality and niche-based processes

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Table S1. Detail of the sampling localities and their year of sampling. Each sampling site was sampled in two distinct seasons: dry and wet season.

Site	**Coordinates**	**Elevation (m a.s.l.)**	**Description**	**Sampling year**
Drink Garri	N 04.1022º, E 09.1225º	650	Lowland forest, minimally disturbed by elephants, where trees of the subfamily Caesalpinioideae (Family: Fabaceae) prevail	2018-2019
PlanteCam	N 4.1175º, E 09.0717º	1100	Mid-elevation forest, partly disturbed by elephants, where *Kigelia africana*, *Macaranga occidentalis* and *Voacanga africana* are common	2018-2019
Crater Lake	N 04.1443º, E 09.0709º	1500	Submontane forest, highly disturbed by elephants, where open elephant pastures are common and where *Aframomum* spp. prevails	2019-2020
Mann's Spring	N 04.1428º, E 09.0630º	2200	Montane forest, close to the timberline, where elephant disturbance is absent and where montane species like *Syzigium staudtii*, *Nuxia congesta* and *Schefflera* spp. are common	2019-2020

Table S2. Functional traits of birds and plants used in the study with details of the classes used and further information on how where they measured, collected or defined.

Plant Traits	**Class or unit of measurements**	**Trait description**
Floral morphology		
Tube length	mm	Length of nectar tube
Tube width	mm	Measured at the entrance of the nectar tube
Final size	Total corolla size (mm)	Zygomorphic flowers were measured both vertically and horizontally
Symmetry	Actinomorphic / Zygomorphic	
Anther position	Exposed / Partially exposed / Hidden	
Flower position	Horizontal / Pendant / Upright / All	Species whose flowers were found to be placed in all three directions were categorised as “All”
Pollinator attraction		
Nectar concentration	w/w %	Measured with pocket refractometer in the field
Nectar volume	µL	
Sugar content	mg	mg of sugar per flower
Odour	None / Weak / Strong	Characterized by the observer
Plant’s life form		
Climber		Species which grows upwards by twining
Epiphyte		Species which grows on top other plants
Herb		Non-woody plant species
Shrub		Plants up to 3 m high
Tree		Plants higher than 3 m

Bird traits	**Class or unit of measurements**	**Trait description**
Bill length	mm	Length from the tip of the bill to the base of the skull
Bill width	mm	Width of the bill at the anterior edge of the nostrils
Bill depth	mm	Depth of the bill at the anterior edge of the nostrils
Weight	g	

Table S3. Frequency of visitation and percentage of robbing (robbing events/visits) recorded in the study at each location and season. The method with which each interaction was recorded is also shown. Plant names follow the International Plant Name Index (IPNI). The abbreviation of bird names takes the first three letters of each name from the scientific name.

Sampling site	Season	Plant species	Method	Bird species	Abbreviation	Frequency	Robbing
Drink Garri	Dry	*Anthonota. fragrans*	Observation	*Anthodiaeta collaris*	ANTCOL	0.157	-
				Anthodiaeta rectirostris	ANTREC	0.718	-
				Anthreptes seimundi	ANTSEI	0.022	-
				Chalcomitra rubescens	CHARUB	0.673	-
				Cinnyris batesi	CINBAT	0.336	-
				Cinnyris minullus	CINMIN	0.426	-
				Cyanomitra cyanolaema	CYACYA	1.144	-
				Cyanomitra olivacea	CYAOLI	2.714	-
		Aframomum sp.	Camera	*Cyanomitra olivacea*	CYAOLI	0.713	100.0
		Berlinia bracteosa	Observation	*Chalcomitra rubescens*	CHARUB	0.195	-
				Cinnyris johannae	CINJOH	0.065	-
				Cyanomitra olivacea	CYAOLI	0.130	-
		Heinsia crinita	Camera	*Anthodiaeta collaris*	ANTCOL	0.078	-
		Hugonia micans	Camera	*Anthodiaeta collaris*	ANTCOL	0.219	-
				Anthreptes rectirostris	ANTREC	0.083	-
				Anthreptes seimundi	ANTSEI	0.031	-
				Chalcomitra rubescens	CHARUB	0.115	-
				Cinnyris batesi	CINBAT	0.073	-
				Cinnyris minullus	CINMIN	0.010	-
				Cyanomitra cyanolaema	CYACYA	0.052	-
		Impatiens niamniamensis	Camera	*Cyanomitra olivacea*	CYAOLI	0.615	35.0
		Sabicea pilosa	Camera	*Cyanomitra olivacea*	CYAOLI	5.596	52.7
		Tabernaemontana brachyantha	Observation	*Cinnyris minullus*	CINMIN	0.175	-
Drink Garri	Wet	*Bertiera racemosa*	Camera	*Cyanomitra olivacea*	CYAOLI	0.035	-
		Clerodendrum sylvaticum	Camera	*Cyanomitra olivacea*	CYAOLI	0.261	-
		Impatiens niamniamensis	Camera	*Cyanomitra olivacea*	CYAOLI	1.076	28.6
				Cyanomitra oritis	CYAORI	0.307	-
		Leea guineensis	Camera	*Cyanomitra olivacea*	CYAOLI	0.450	-

		Phragmanthera kamerunensis	Observation	*Chalcomitra rubescens*	CHARUB	0.022	-
				Cinnyris johannae	CINJOH	0.389	13.9
				Cinnyris. minullus	CINMIN	0.194	44.4
				Cyanomitra olivacea	CYAOLI	0.324	10.0
PlanteCam	Dry	*Aframomum sp.*	Camera	*Cyanomitra oritis*	CYAORI	0.126	33.0
		Anthonotha fragans	Observation	*Anthodiaeta collaris*	ANTCOL	0.398	-
				Anthreptes rectirostris	ANTREC	0.133	-
				Cinnyris ursulae	CINURS	3.712	-
				Cyanomitra olivacea	CYAOLI	0.795	-
				Cyanomitra oritis	CYAORI	0.133	
		Cordia aurantiaca	Camera	*Cinnyris ursulae*	CINURS	0.709	-
		Costus dubius	Camera	*Cyanomitra olivacea*	CYAOLI	0.012	-
		Dischistocalyx grandifolius	Observation	*Cyanomitra oritis*	CYAORI	0.015	-
		Impatiens niamniamensis	Camera	*Cinnyris ursulae*	CINURS	0.007	-
				Cyanomitra olivacea	CYAOLI	0.017	100.0
				Cyanomitra oritis	CYAORI	0.017	-
		Kigelia africana	Observation	*Anthodiaeta collaris*	ANTCOL	0.277	-
				Cinnyris ursulae	CINURS	40.294	-
				Cyanomitra olivacea	CYAOLI	3.185	-
				Cyanomitra oritis	CYAORI	21.462	-
		Pavetta rigida	Camera	*Cyanomitra olivacea*	CYAOLI	0.013	-
		Sabicea pilosa	Camera	*Cinnyris ursulae*	CINURS	0.093	8.3
				Cyanomitra olivacea	CYAOLI	0.255	30.3
		Schumanniophyton magnificum	Camera	*Cyanomitra olivacea*	CYAOLI	0.007	-
		Sherbournia bignoniiflora	Camera	*Cyanomitra olivacea*	CYAOLI	0.004	-
				Cyanomitra oritis	CYAORI	0.026	-
		Tabernaemontana ventricosa	Observation	*Anthodiaeta collaris*	ANTCOL	1.500	-
				Cinnyris ursulae	CINURS	9.500	-
				Cyanomitra olivacea	CYAOLI	1.000	-
				Cyanomitra oritis	CYAORI	0.667	-
		Voacanga africana		*Anthodiaeta collaris*	ANTCOL	0.781	-
				Cinnyris ursulae	CINURS	0.781	-
				Cyanomitra oritis	CYAORI	0.260	-
PlanteCam	Wet	*Costus dubius*	Camera	*Cinnyris reichenowi*	CINREI	0.290	97.6
		Impatiens etiendensis	Camera	*Cyanomitra oritis*	CYAORI	0.016	-
		Impatiens frithii	Camera	*Cinnyris reichenowi*	CINREI	0.043	-
				Cinnyris ursulae	CINURS	0.043	-

				Cyanomitra oritis	CYAORI	0.652	-
		Impatiens hians	Camera	*Cinnyris reichenowi*	CINREI	0.006	100
				Cyanomitra oritis	CYAORI	0.007	10.0
		Impatiens niamniamensis	Camera	*Cinnyris reichenowi*	CINREI	1.539	100.0
				Cyanomitra oritis	CYAORI	1.129	-
		Mussaenda tenuiflora	Observation	*Cyanomitra oritis*	CYAORI	0.007	-
		Plectranthus decurrens	Camera	*Cinnyris reichenowi*	CINREI	0.125	-
		Thonningia sanguinea	Camera	*Cinnyris reichenowi*	CINREI	0.040	-
				Cyanomitra olivacea	CYAORI	0.024	-
				Cyanomitra oritis	CYAORI	2.951	1.37
		Thunbergia fasciculata	Camera	*Cinnyris reichenowi*	CINREI	0.093	100.0
				Cyanomitra olivacea	CYAOLI	0.031	-
Crater Lake	Dry	*Acanthopale decempedalis*	Camera	*Cyanomitra reichenowi*	CINREI	0.122	66.0
		Aframomum sp.	Camera	*Cyanomitra oritis*	CYAORI	0.333	54.5
		Aframomum sp.	Camera	*Cyanomitra oritis*	CYAORI	1.220	2.3
		Brillantaisia owariensis	Camera	*Cinnyris reichenowi*	CINREI	0.123	-
				Cyanomitra oritis	CYAORI	0.022	-
		Costus dubius	Camera	*Cinnyris reichenowi*	CINREI	0.003	-
				Cyanomitra oritis	CYAORI	0.035	
		Dicranolepis vestita	Observation	*Cinnyris reichenowi*	CINREI	18.477	-
		Englerina gabonensis	Observation	*Cinnyris reichenowi*	CINREI	0.742	10.5
				Cyanomitra oritis	CYAORI	4.063	-
		Impatiens burtonii	Camera	*Cinnyris reichenowi*	CINREI	0.006	100.0
		Impatiens niamniamensis	Camera	*Cinnyris reichenowi*	CINREI	0.024	100.0
				Cyanomitra oritis	CYAORI	0.098	4.0
		Ixora guineensis	Camera	*Cinnyris reichenowi*	CINREI	0.208	-
		Kigelia africana	Observation	*Cinnyris reichenowi*	CINREI	5.648	34.8
				Cyanomitra oritis	CYAORI	10.294	16.8
		Mimulopsis solmsii	Camera	*Cinnyris reichenowi*	CINREI	0.044	50.0
				Cyanomitra oritis	CYAORI	0.022	-
		Mussaenda tenuiflora	Observation	*Cinnyris reichenowi*	CINREI	0.367	4.8
				Cyanomitra oritis	CYAORI	0.031	-
		Phragmenthera kamerunensis	Camera	*Cinnyris reichenowi*	CINREI	0.106	14.3
		Psydrax dunlapii	Observation	*Cinnyris reichenowi*	CINREI	2.551	-
				Cyanomitra oritis	CYAORI	0.091	-
		Syzigium sp.	Observation	*Cinnyris reichenowi*	CINREI	50.859	-
				Cyanomitra oritis	CYAORI	1.367	-
		Tabernaemontana ventricosa	Observation	*Cinnyris reichenowi*	CINREI	154.297	-
				Cyanomitra oritis	CYAORI	10.742	-

		Thonningia sanguinea	Camera	*Cyanomitra oritis*	CYAORI	0.161	-
Crater Lake	Wet	*Acanthopale decempedalis*	Camera	*Cinnyris reichenowi*	CINREI	0.034	-
		Aframomum sp.	Camera	*Cyanomitra oritis*	CYAORI	0.117	100.0
		Aframomum sp.	Camera	*Cinnyris reichenowi*	CINREI	0.008	100.0
				Cyanomitra oritis	CYAORI	0.265	5.6
		Anthocleista scandens	Observation	*Cinnyris reichenowi*	CINREI	4.609	-
				Cyanomitra oritis	CYAORI	19.688	-
		Clerodendrum sylvaticum	Camera	*Cinnyris reichenowi*	CINREI	0.508	-
		Costus dubius	Camera	*Cyanomitra oritis*	CYAORI	0.118	-
		Impatiens etindensis	Camera	*Cinnyris reichenowi*	CINREI	0.773	7.4
				Cyanomitra oritis	CYAORI	0.544	-
		Impatiens niamniamensis	Camera	*Cinnyris reichenowi*	CINREI	3.569	95.2
				Cyanomitra oritis	CYAORI	0.685	-
		Ixora guineensis	Camera	*Cyanomitra oritis*	CYAORI	0.066	-
		Mussaenda tenuiflora	Observation	*Cinnyris reichenowi*	CINREI	0.210	19.2
		Plectranthus kamerunensis		*Cinnyris reichenowi*	CINREI	0.376	-
				Cyanomitra oritis	CYAORI	0.075	-
		Thonningia sanguinea		*Cyanomitra oritis*	CYAORI	28.766	-
Mann's Spring	Dry	*Acanthopale decempedalis*	Camera	*Cinnyris reichenowi*	CINREI	0.623	-
		Clausena anisata	Camera	*Cinnyris reichenowi*	CINREI	0.391	-
				Cyanomitra oritis	CYAORI	0.031	-
		Hypoestes triflora	Camera	*Cinnyris reichenowi*	CINREI	0.134	-
		Impatiens sakeriana	Camera	*Cinnyris reichenowi*	CINREI	0.152	10.0
				Cyanomitra oritis	CYAORI	0.236	-
		Nuxia congesta	Observation	*Cinnyris reichenowi*	CINREI	39.461	-
				Cyanomitra oritis	CYAORI	1.561	
		Psydrax dunlapii	Observation	*Cinnyris reichenowi*	CINREI	6.159	-
				Cyanomitra oritis	CYAORI	0.143	-
		Schefflera abyssinica	Observation	*Cinnyris reichenowi*	CINREI	11.275	-
				Cyanomitra oritis	CYAORI	1.126	-
		Syzigium staudtii	Observation	*Cinnyris reichenowi*	CINREI	9.583	-
				Cyanomitra oritis	CYAORI	0.104	-
Mann's Spring	Wet	*Acanthopale decempedalis*	Camera	*Cinnyris reichenowi*	CINREI	2.209	78.6
				Cyanomitra oritis	CYAORI	0.126	
		Chassalia laikomensis	Camera	*Cyanomitra oritis*	CYAORI	0.064	50.0
		Impatiens sakeriana	Camera	*Cinnyris reichenowi*	CINREI	0.725	-
				Cyanomitra oritis	CYAORI	0.062	-
		Jasminum preussii	Camera	*Cinnyris reichenowi*	CINREI	0.543	4.54
		Psychotria hypsophila	Camera	*Cinnyris reichenowi*	CINREI	52.794	-
		Rhipidoglossum sp.	Camera	*Cinnyris reichenowi*	CINREI	0.164	-

Table S4. β-diversity of interactions for the season-based matrices with robbing. The interaction turnover (βWN) was split in its two components: species turnover (βST) and interaction rewiring (βOS). Further βST was partitioned into the effects of the lower (βST low), higher (βST high) or both levels (βST lh) of the bipartite networks. The effects of species replacement (βWN rep / βOS rep) and richness (βWN rich / βOS rich) on βWN and βOS are also shown.

Seasonal *β*-diversity of interactions				
β_{WN}	0.718	$\beta_{WN\ rep}$ 0.400	$\beta_{WN\ rich}$ 0.318	
β_{ST}	0.682	$\beta_{ST\ low}$ 0.459	$\beta_{ST\ high}$ 0.000	$\beta_{ST\ lh}$ 0.224
β_{OS}	0.035	$\beta_{OS\ rep}$ 0.024	$\beta_{OS\ rich}$ 0.012	

Table S5. Forward selection analysis for the full matrix including robbing events: a) Summary of the results from the Redundancy Analysis (RDA); b) Bird traits tested: bill length, weight, and width and depth of the bill. Their significance was tested with 999 Monte Carlo permutations.

a) Summary of the Redundancy Analysis results

Total variation	% Contribution of explanatory variables	Adj. method	Adj. % explained variation
231.00	52.8	FDR	21.64

Eigenvalue decomposition

Axis	**1**	**2**	**3**	**4**
Value	0.3048	0.1738	0.0349	0.0163
Cumulative variation	30.48	47.86	51.35	52.98
P-canonical correlation	0.9530	0.7515	0.7301	0.385
Explained fitted variation	57.73	90.33	96.91	100.00

b) Variables tested

Trait	Explained variability	% Contribution	Pseudo-F	p-value	p-value adj.
Bill length	23.0	43.4	2.7	0.021	0.084
Weight	12.1	22.8	1.5	0.213	0.426
Bill width	12.9	24.4	1.7	0.126	0.252
Bill depth	5.0	9.3	0.6	0.730	0.730

Table S6. Forward selection analysis for the dry season matrix without robbing: a) Summary of the results from the Redundancy Analysis (RDA); b) Bird traits tested: bill length, weight, and width and depth of the bill. Their significance was tested with 999 Monte Carlo permutations.

a) Summary of the Redundancy Analysis results

Total variation	% Contribution of explanatory variables	Adj. method	Adj. % explained variation
210.00	50.21	FDR	10.38

Eigenvalue decomposition

Axis	1	2	3	4
Value	0.4064	0.0599	0.0253	0.0105
Cumulative variation	40.64	46.63	49.16	50.21
P-canonical correlation	0.8901	0.6945	0.3841	0.3602
Explained fitted variation	80.93	92.86	97.90	100.00

b) Variables tested

Trait	Explained variability	% Contribution	Pseudo-F	p-value	p-value adj.
Bill length	19.9	39.7	2.0	0.116	0.463
Weight	17.5	34.8	2.0	0.128	0.257
Width	11.0	21.9	1.3	0.306	0.408
Depth	1.8	3.6	0.2	0.988	0.988

Table S7. Forward selection analysis for the wet season matrix without robbing: a) Summary of the results from the Redundancy Analysis (RDA); b) Bird traits tested: Length of the bill, bird weight, and width and depth of the bill. Only those bird traits that accounted for all the variability in the dataset are shown. Their significance was tested with 999 Monte Carlo permutations.

Total variation	**% Contribution of explanatory variables**	**Adj. method**	**Adj. % explained variation**
80.00	100.00	FDR	0.00

Axis	**1**	**2**	**3**
Value	0.4625	0.4052	0.1323
Cumulative variation	46.25	86.77	100.00
P-canonical correlation	1.00	1.00	1.00
Explained fitted variation	0.00	0.00	0.00

Trait	**Explained variability**	**% Contribution**	**Pseudo-F**	**p-value**	**p-value adj.**
Weight	20.3	20.3	0.5	0.702	1.000
Width	37.8	37.8	<0.1	1.000	1.000
Depth	41.9	41.9	1.4	0.138	0.523

Table S8. Forward selection analysis for the dry season matrix with robbing: a) Summary of the results from the Redundancy Analysis (RDA); b) Bird traits tested: Length of the bill, bird weight, and width and depth of the bill. Their significance was tested with 999 Monte Carlo permutations.

a) Summary of the Redundancy Analysis results

Total variation	% Contribution of explanatory variables	Adj. method	Adj. % explained variation	
210.00	53.90	FDR	17.02	
Eigenvalue decomposition				
Axis	**1**	**2**	**3**	**4**
Value	0.4475	0.0581	0.0257	0.0076
Cumulative variation	44.75	50.57	53.14	53.90
P-canonical correlation	0.9102	0.7044	0.3814	0.3551
Explained fitted variation	83.03	93.81	98.58	100.00

b) Variables tested

Trait	Explained variability	% Contribution	Pseudo-F	p-value	p-value adj.
Bill length	21.8	40.5	2.2	0.089	0.359
Weight	17.6	32.7	2.0	0.104	0.207
Width	2.0	3.7	0.2	0.992	0.992
Depth	12.5	23.1	1.6	0.204	0.272

Table S9. Forward selection analysis for the wet season matrix with robbing: a) Summary of the results from the Redundancy Analysis (RDA); b) Bird traits tested: Length of the bill, bird weight, and width and depth of the bill. Only those bird traits that accounted for all the variability in the dataset are shown. Their significance was tested with 999 Monte Carlo permutations.

Total variation	% Contribution of explanatory variables	Adj. method	Adj. % explained variation
100.00	100.00	FDR	0.00

Axis	1	2	3
Value	0.5402	0.3152	0.1446
Cumulative variation	54.02	85.54	100.00
P-canonical correlation	1.00	1.00	1.00
Explained fitted variation	0.00	0.00	0.00

Trait	Explained variability	% Contribution	Pseudo-F	p-value	p-value adj.
Bill length	30.4	30.4	<0.1	1.000	1.000
Weight	33.2	33.2	1.1	0.560	0.933
Width	27.3	27.3	0.9	0.517	1.000
Depth	9.0	9.0	0.3	1.000	1.000

Table S10. Results from the modelling of bird feeding niches (with robbing events) and its comparison with the observed values. Mean observed Euclidean distance (Obs. Dist.) and null modelled mean Euclidean distance (N. Dist.) for all the matrices analysed.

Modelling of bird feeding niches

Matrix	***Obs. Dist.***	***N. Dist.***	***p-value***
Full	5.504	6.125	< 0.05
Wet	4.832	6.204	< 0.05
Dry	5.358	6.077	< 0.05

Table S11. Results of pairwise comparisons of sunbirds species in which the observed Euclidean distance (Obs. Dist) and the null modelled one (N. Dist.) was significant for the full matrix excluding robbing events. Bird names are abbreviated as in Table S3.

Sunbirds	***Obs. Dist.***	***N. Dist.***	***p-value***
Antcol-Cyaoli	5.929	4.842	0.026
Antcol-Cyaori	6.579	1.023	0.005
Antcol-Cinrei	4.585	7.010	0.002
Antrec-Cyacya	0.069	3.000	0.047
Antrec-Cyaoli	5.838	4.000	0.048
Antrec-Cinrei	6.036	6.738	0.009
Charub-Cinrei	5.783	6.877	0.003
Cinbat-Cinrei	5.711	7.176	0.003
Cyacya-Cinrei	6.064	6.862	0.018
Cyaoli-Cyaori	5.886	4.561	0.014
Cyaoli-Cinurs	5.937	6.611	0.000
Cinmin-Cinrei	6.232	7.376	0.021

Table S12. Results of pairwise comparisons of sunbirds species in which the observed Euclidean distance (Obs. Dist) and the null modelled one (N. Dist.) was significant for the full matrix including robbing events. Bird names are abbreviated as in Table S3.

Sunbirds	***Obs. Dist.***	***N. Dist.***	***p-value***
Antcol-Cyaoli	6.018	3.677	0.002
Antcol-Cyori	6.802	0.749	0.004
Antcol-Cinurs	8.357	7.356	0.018
Antcol-Cinrei	4.46	7.168	0.000
Antrec-Cyacya	0.072	2.941	0.031
Antrec-Cyaoli	6.267	3.958	0.011
Charub-Cinrei	5.868	7.129	0.014
Cinbat-Cinrei	5.389	7.439	0.004
Cyacya-Cyaoli	6.308	4.153	0.015
Cyaoli-Cinjoh	7.574	6.525	0.034
Cyaoli-Cyaori	4.836	3.45	0.001
Cyaoli-Cinurs	5.686	6.126	0.011
Cinmin-Cinrei	5.779	7.399	0.004

Table S13. Results of pairwise comparisons of sunbirds species in which the observed Euclidean distance (Obs. Dist) and the null modelled one (N. Dist.) was significant for the dry season matrix excluding robbing events. Bird names are abbreviated as in Table S3.

Sunbirds	***Obs. Dist.***	***N. Dist.***	***p-value***
Antcol-Cyaoli	7.797	5.699	0.011
Antcol-Cinurs	8.237	1.494	0.008
Antcol-Cyaori	7.212	5.434	0.007
Antcol-Cinrei	5.228	8.441	0.004
Antrec-Cyacya	0.084	3.516	0.044
Antrec-Cyaoli	7.703	4.002	0.004
Charub-Cyaoli	7.168	4.329	0.027
Cinbat-Cyaoli	7.092	5.017	0.037
Cyacya-Cyaoli	7.750	4.288	0.002
Cyaoli-Cinmin	8.025	5.454	0.005
Cyaoli-Cinurs	7.907	5.400	0.006
Cyaoli-Cyaori	6.182	4.880	0.009
Cinurs-Cyaori	2.718	4.612	0.000
Cyaori-Cinrei	5.967	4.300	0.000

Table S14. Results of pairwise comparisons of sunbirds species in which the observed Euclidean distance (Obs. Dist) and the null modelled one (N. Dist.) was significant for the dry season matrix including robbing events. Bird names are abbreviated as in Table S3.

Sunbirds	***Obs. Dist.***	***N. Dist.***	***p- value***
Antcol-Cyaoli	8.074	4.589	0.000
Antcol-Cinurs	8.374	1.151	0.004
Antcol-Cyaori	7.197	5.208	0.002
Antcol-Cinrei	5.311	8.333	0.002
Antrec-Cyacya	0.101	3.606	0.038
Antrec-Cyaoli	8.237	4.917	0.001
Cinbat-Cyaoli	7.571	5.685	0.028
Cyacya-Cyaoli	8.290	5.113	0.001
Cyaoli-Cinmin	8.603	5.968	0.005
Cyaoli-Cinurs	6.864	4.382	0.001
Cinurs-Cyaori	2.775	4.550	0.000
Cyaori-Cinrei	5.990	4.351	0.000

Table S15. Results of pairwise comparisons of sunbirds species in which the observed Euclidean distance (Obs. Dist) and the null modelled one (N. Dist.) was significant for the wet season matrices a) excluding robbing events; b) including robbing events. Bird names are abbreviated as in Table S3.

a) Without robbing

Sunbirds	***Obs. Dist.***	***N. Dist.***	***p- value***
Cinjoh-Cinrei	6.812	6.028	0.022
Cyaoli-Cyaori	6.462	7.299	0.002
Cyaori-Cinrei	7.449	7.108	0.020

b) With robbing

Sunbirds	***Obs. Dist.***	***N. Dist.***	***p- value***
Cyaori-Cinrei	7.807	7.474	0.025

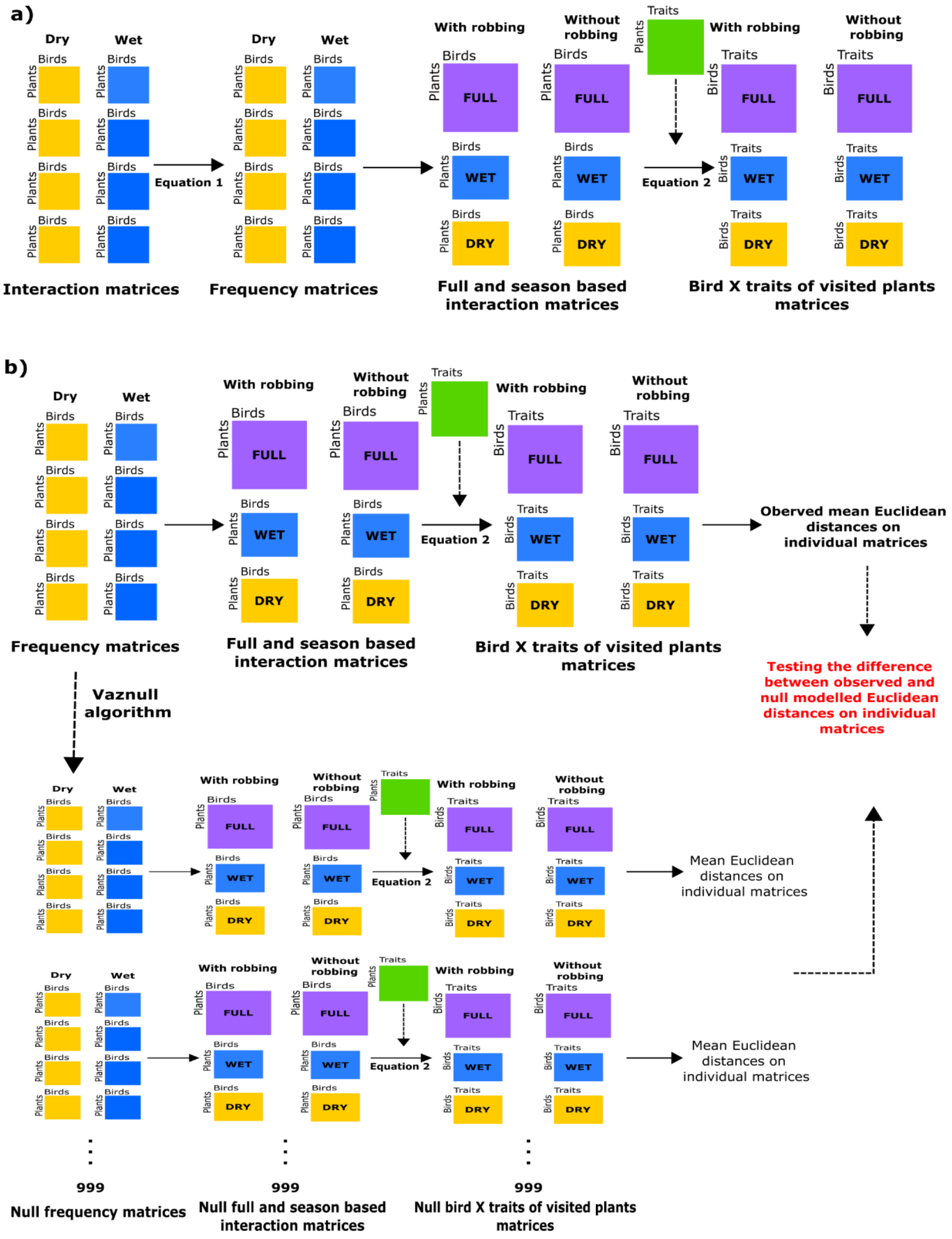

a)
Dry
Wet
Birds
Plants
Equation 1
Interaction matrices
Frequency matrices
With robbing
Without robbing
Traits
FULL
WET
DRY
Equation 2
Full and season based interaction matrices
Bird X traits of visited plants matrices
b)
Frequency matrices
Full and season based interaction matrices
Bird X traits of visited plants matrices
Oberved mean Euclidean distances on individual matrices
Testing the difference between observed and null modelled Euclidean distances on individual matrices
Vaznull algorithm
Mean Euclidean distances on individual matrices
999
Null frequency matrices
Null full and season based interaction matrices
Null bird X traits of visited plants matrices

Figure S1. Conceptualization of the methods used in the study. a) Construction of bird * traits matrices of visited plants from the interaction matrices; b) modelling of bird feeding niche using "*Vaznull* algorithm" and a Euclidean distance approach. The observed frequency matrices were null modelled. Then they were compound into full and seasonal matrices. To this end, the null Euclidean distance matrices were calculated and compared to the observed ones.

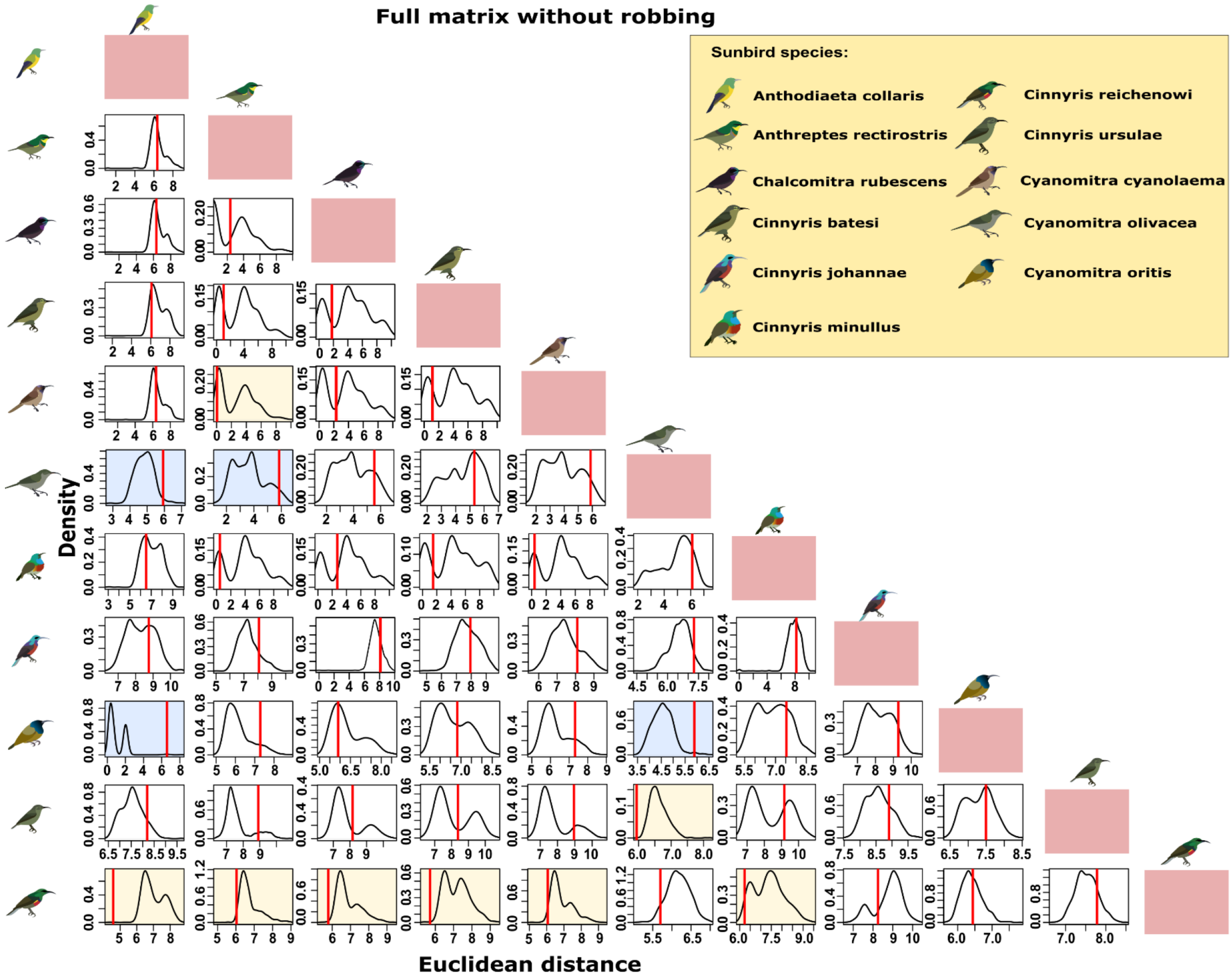
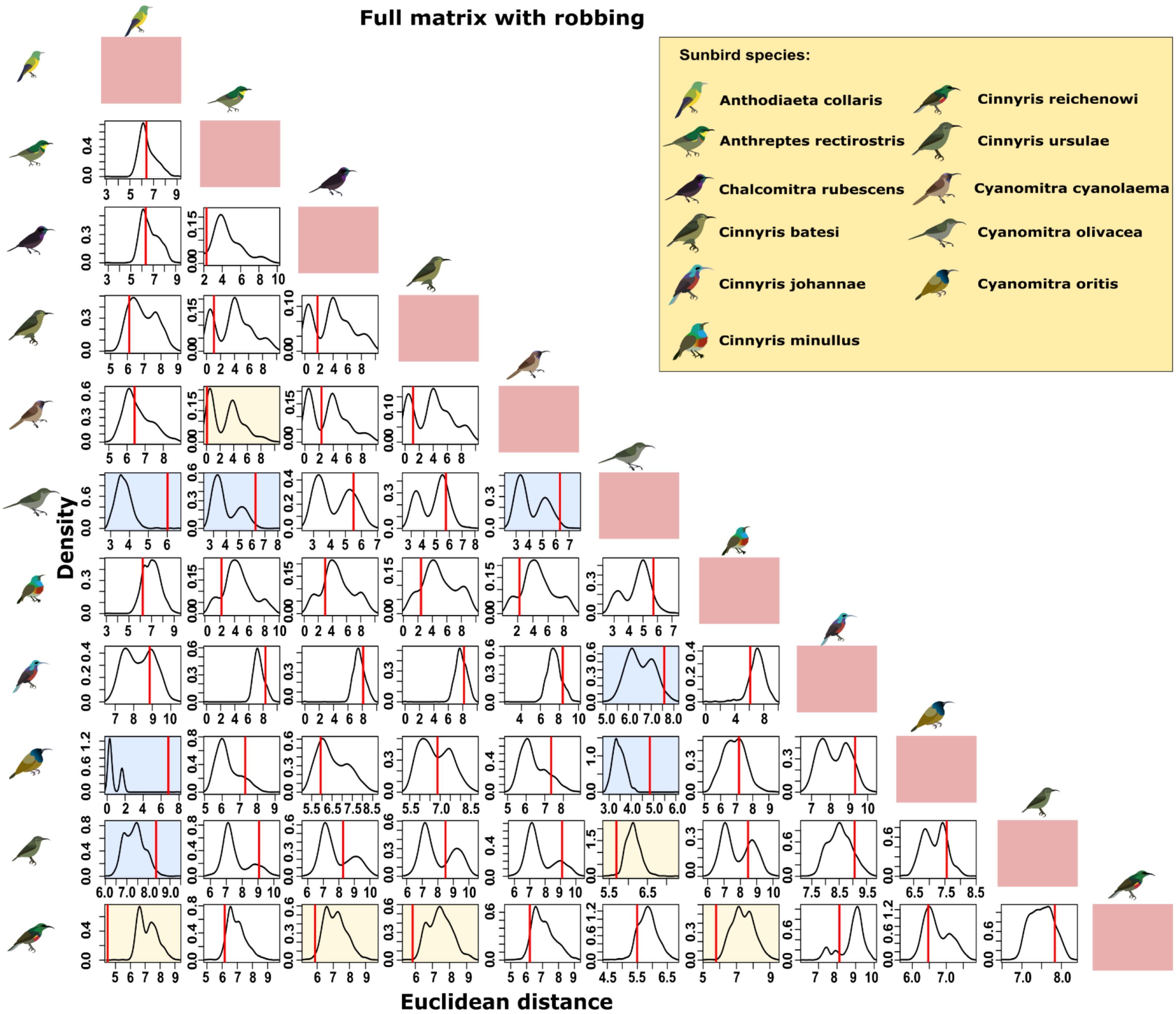

Full matrix without robbing
Sunbird species:
Anthodiaeta collaris
Anthreptes rectirostris
Chalcomitra rubescens
Cinnyris batesi
Cinnyris johannae
Cinnyris minullus
Cinnyris reichenowi
Cinnyris ursulae
Cyanomitra cyanolaema
Cyanomitra olivacea
Cyanomitra oritis
Density
Euclidean distance

Figure S2. Analysis of the bird feeding niches for the full matrix excluding the robbing events. Each plot shows the distribution of modelled Euclidean distances according to visited plant traits. Red bars represent the observed Euclidean distance among each pair of species. Colored boxes indicate those pairs of species whose observed Euclidean distance was statistically significant (*p-value* < 0.05). In yellow species whose observed Euclidean distance was smaller than expected by chance; in blue those whose observed Euclidean distance was bigger than expected by chance.



Full matrix with robbing

Figure S3. Analysis of the bird feeding niches for the full matrix including robbing events. Each plot shows the distribution of modelled Euclidean distances according to visited plant traits. Red bars represent the observed Euclidean distance among each pair of species. Colored boxes indicate those pairs of species whose observed Euclidean distance was statistically significant (*p-value* < 0.05). In yellow species whose observed Euclidean distance was smaller than expected chance; in blue those whose observed Euclidean distance was bigger than expected by chance.

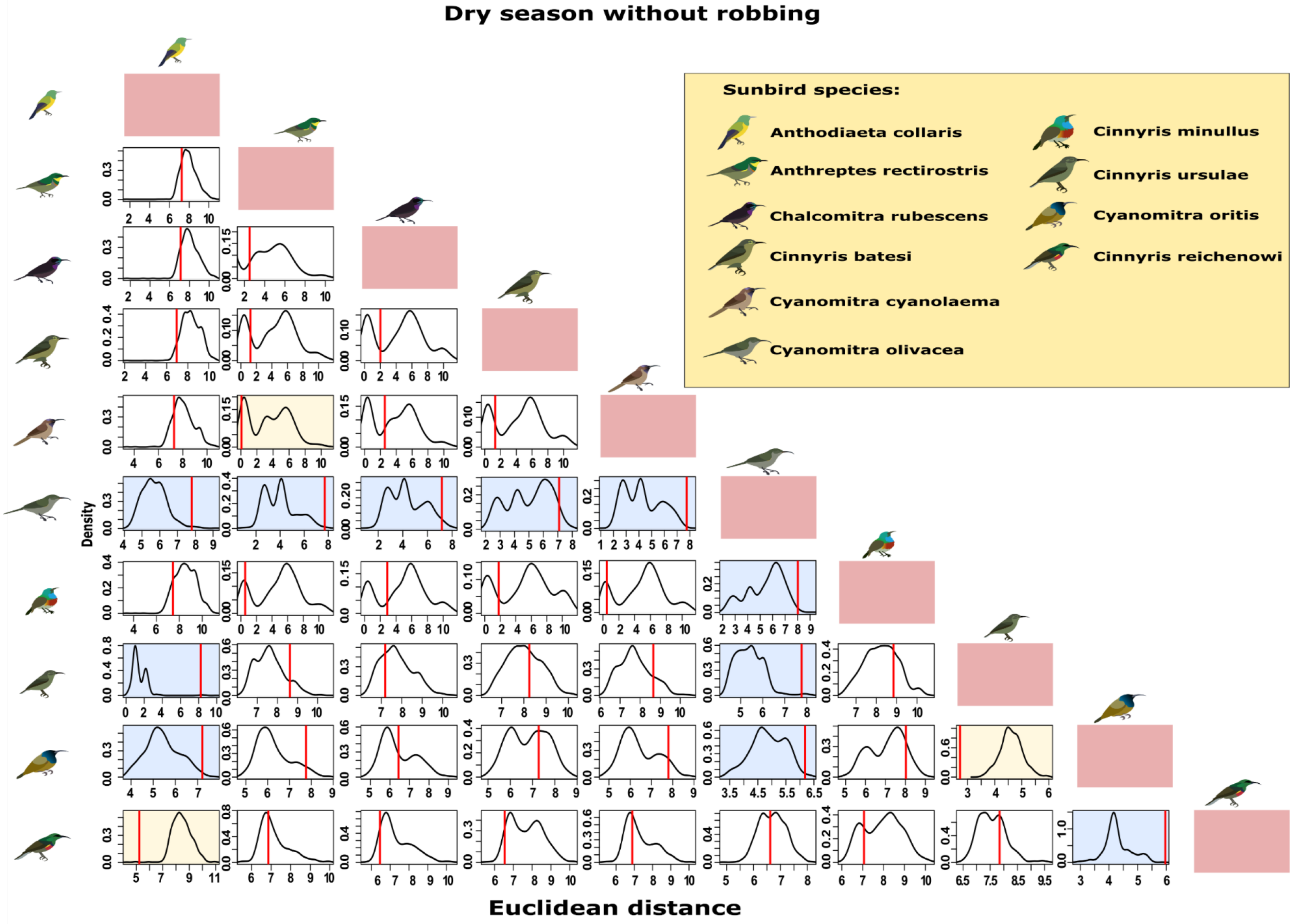
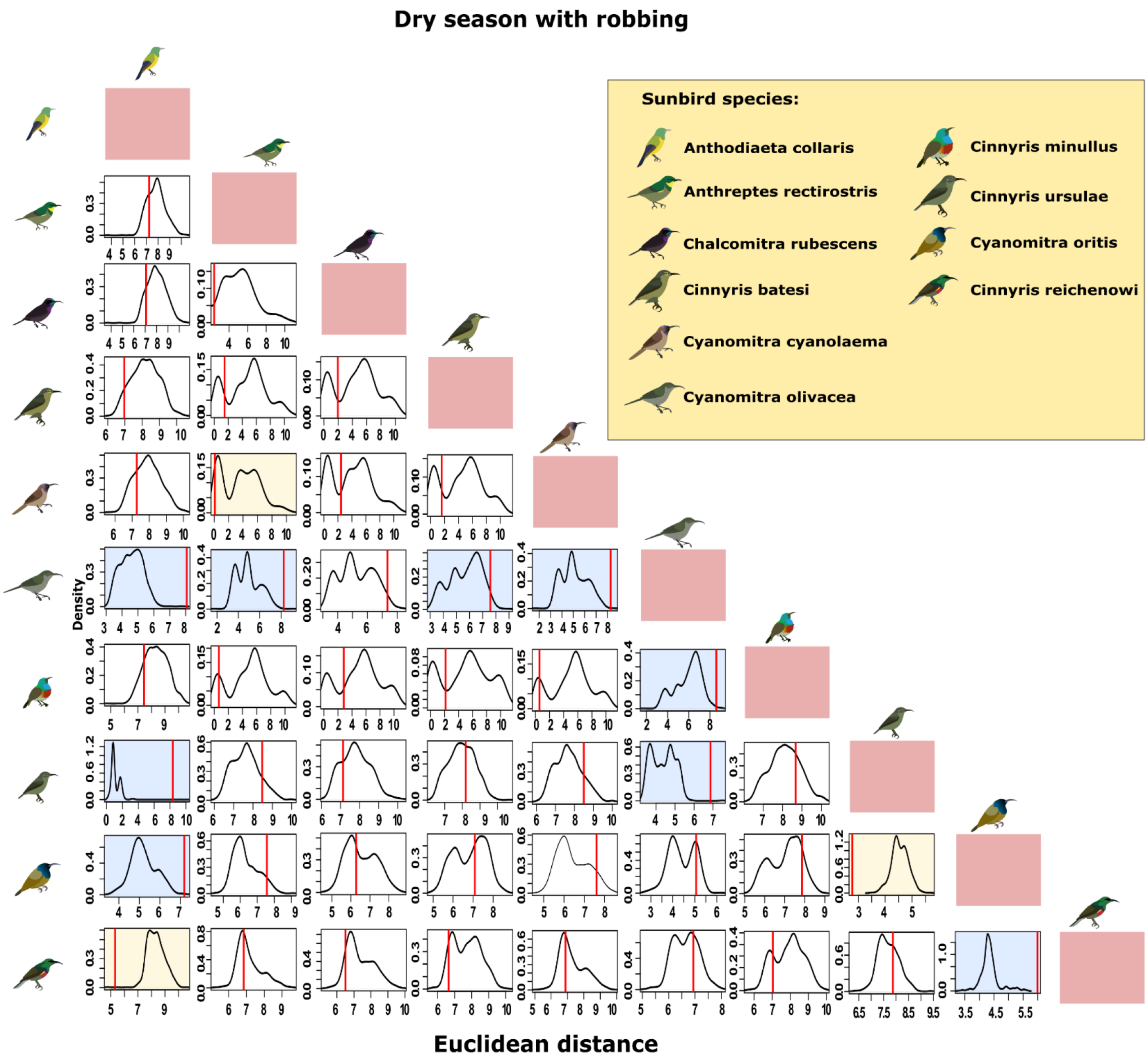

Dry season without robbing
Sunbird species:
Anthodiaeta collaris
Anthreptes rectirostris
Chalcomitra rubescens
Cinnyris batesi
Cyanomitra cyanolaema
Cyanomitra olivacea
Cinnyris minullus
Cinnyris ursulae
Cyanomitra oritis
Cinnyris reichenowi
Density
Euclidean distance

Figure S4. Analysis of the bird feeding niches for the dry season matrix excluding the robbing events. Each plot shows the distribution of modelled Euclidean distances according to visited plant traits. Red bars represent the observed Euclidean distance among each pair of species. Colored boxes indicate those pairs of species whose observed Euclidean distance was statistically significant (*p-value* < 0.05). In yellow species whose observed Euclidean distance was smaller than expected chance; in blue those whose observed Euclidean distance was bigger than expected by chance.



Dry season with robbing
Sunbird species:
Anthodiaeta collaris
Anthreptes rectirostris
Chalcomitra rubescens
Cinnyris batesi
Cyanomitra cyanolaema
Cyanomitra olivacea
Cinnyris minullus
Cinnyris ursulae
Cyanomitra oritis
Cinnyris reichenowi
Density
Euclidean distance

Figure S5. Analysis of the bird feeding niches for the dry season matrix including robbing events. Each plot shows the distribution of modelled Euclidean distances according to visited plant traits. Red bars represent the observed Euclidean distance among each pair of species. Colored boxes indicate those pairs of species whose observed Euclidean distance was statistically significant (*p-value* < 0.05). In yellow species whose observed Euclidean distance was smaller than expected chance; in blue those whose observed Euclidean distance was bigger than expected by chance.

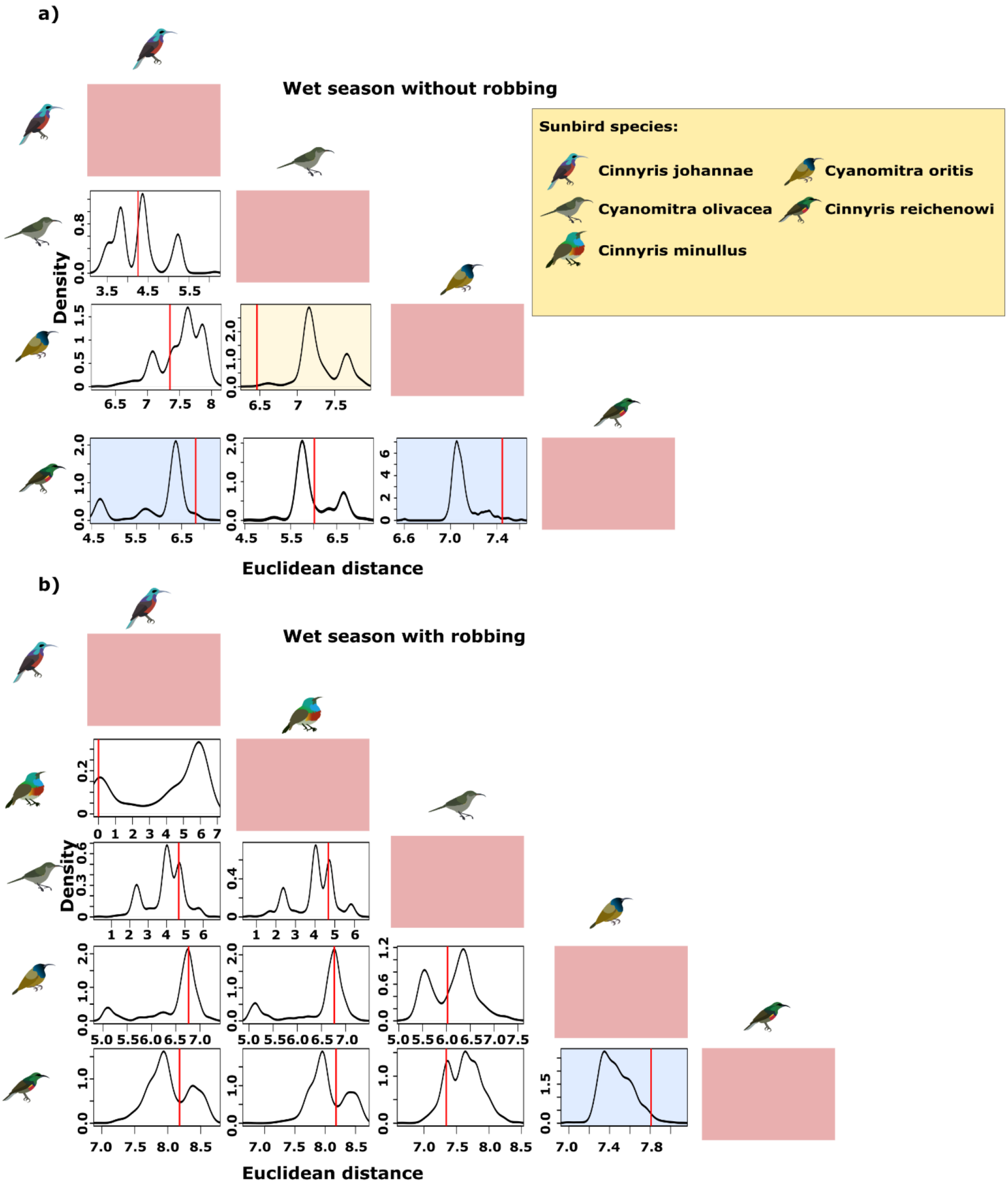

a)
Wet season without robbing
Sunbird species:
Cinnyris johannae
Cyanomitra oritis
Cyanomitra olivacea
Cinnyris reichenowi
Cinnyris minullus
Density
0.0
0.8
3.5
4.5
5.5
0
0.5
1
1.5
6.5
7
7.5
8
0.0
1.0
2.0
6.5
7
7.5
0.0
1.0
2.0
4.5
5.5
6.5
0.0
1.0
2.0
4.5
5.5
6.5
0
2
4
6
6.6
7.0
7.4
Euclidean distance
b)
Wet season with robbing
0
0.2
0 1 2 3 4 5 6 7
Density
0
0.3
0.6
1 2 3 4 5 6
0
0.4
1 2 3 4 5 6
0.0
1.0
2.0
5.0 5.5 6.0 6.5 7.0
0.0
1.0
2.0
5.0 5.5 6.0 6.5 7.0
0.0
0.6
1.2
5.0 5.5 6.0 6.5 7.0 7.5
0.0
1.0
7.0 7.5 8.0 8.5
0.0
1.0
7.0 7.5 8.0 8.5
0.0
1.0
7.0 7.5 8.0 8.5
0.0
1.5
7.0 7.4 7.8
Euclidean distance

Figure S6. Analysis of the bird feeding niches for the wet season matrix: a) excluding robbing events; b) including robbing events. Each plot shows the distribution of modelled Euclidean distances according to visited plant traits. Red bars represent the observed Euclidean distance among each pair of species. Colored boxes indicate those pairs of species whose observed Euclidean distance was statistically significant (*p-value* < 0.05). In yellow species whose observed Euclidean distance was smaller than expected chance; in blue those whose observed Euclidean distance was bigger than expected by chance.

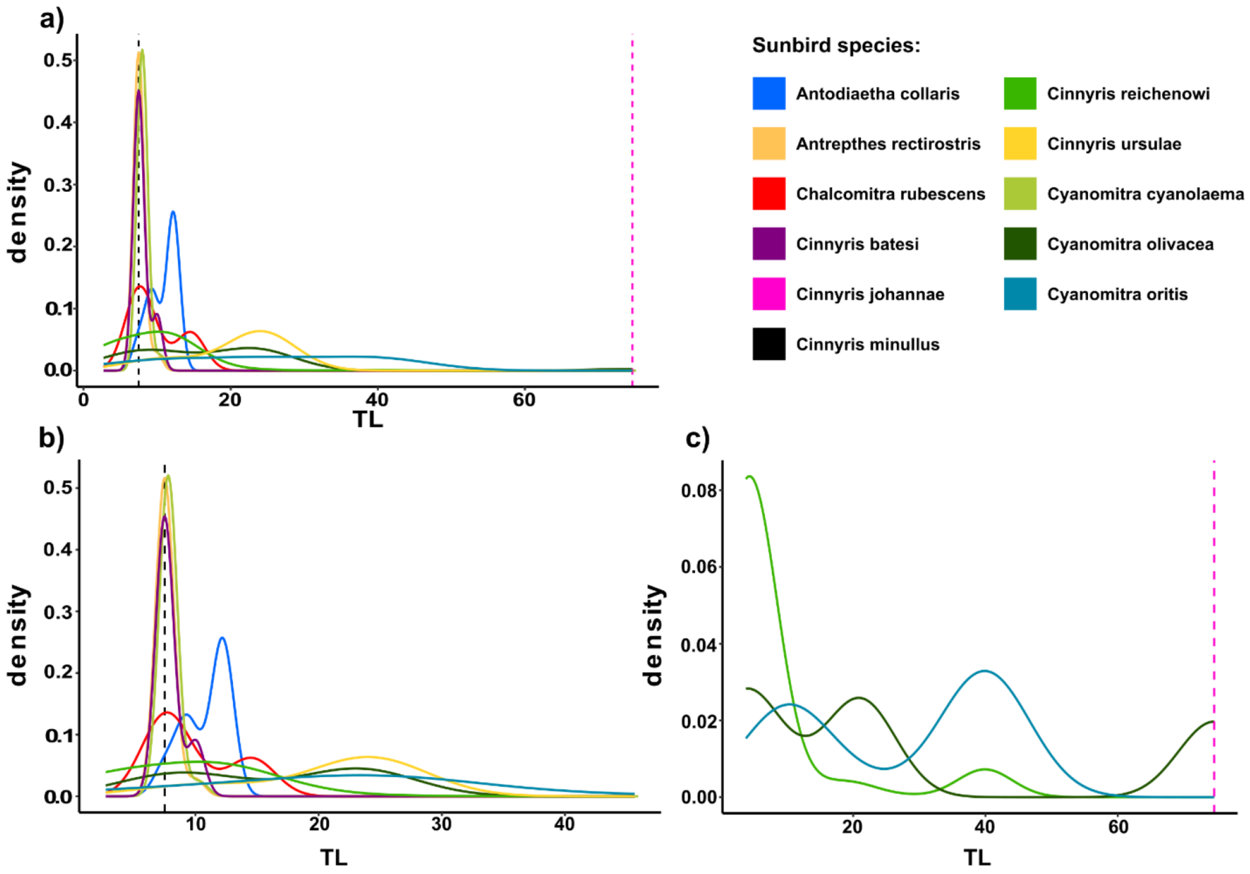


Figure S7. Density plots showing the distribution of tube lengths (TL; in mm) lengths visited by each sunbird species when excluding the robbing events for: a) Full matrix; b) Dry season matrix; c) Wet season matrix. The densities of each tube length are weighted by the interaction frequency of a particular interaction. Interaction frequencies were standardised to one for each sunbird species, so the density curves are comparable.

PART-II BIRD POLLINATION SYNDROME

Cyanomitra oritis

Chapter II

Janeček, Š., Chmel, K., **Uceda Gómez, G.**, Janečková, P., Chmelová, E., Sejfová, S., & Ewome, F.L. (2020). Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution*, 10, 1784–1793. https://doi.org/10.1002/ece3.5942

Chapter III

Mundi, O., Awa II, T., Chmel, K., Ewome, F.L., **Uceda-Gómez, G.**, Janečková, P., & Janeček, Š. (2022). The ornithophily of *Impatiens sakeriana* does not guarantee a preference by sunbirds. *Biological Journal of the Linnean Society*, 137, 240-249. https://doi.org/10.1093/biolinnean/blac083

Chapter IV

Chmel, K., Ewome, F.L., **Uceda Gómez, G.**, Klomberg, Y., Mertens, J.E.J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome works as the plant's adaptation to ornithophily, while nectarivorous birds do not seem to care. *Oikos*, 130, 1411-1424. https://doi.org/10.1111/oik.08052

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ORIGINAL RESEARCH

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Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants

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Abstract

1. Plant–bird pollination interactions evolved independently on different continents. Specific adaptations can lead to their restriction when potential partners from distant evolutionary trajectories come into contact. Alternatively, these interactions can be enabled by convergent evolution and subsequent ecological fitting.
2. We studied the interactions between New World plants from the genus *Heliconia*, Asian plants of genus *Etlingera* and African sunbirds on a local farm in Cameroon. *Heliconia* spp. evolved together with hummingbirds and *Etlingera* spp. with spiderhunters —an oriental subgroup of the sunbird family.
3. Sunbirds fed on all studied plants and individual plant species were visited by a different sunbird spectrum. We experimentally documented a higher number of germinated pollen grains in sunbird-visited flowers of *Etlingera* spp. For *Heliconia* spp., this experiment was not successful and pollen tubes were rarely observed, even in hand-pollinated flowers, where enough pollen was deposited. The analyses of contacts with plant reproductive organs nevertheless confirmed that sunbirds are good pollen vectors for both *Heliconia* and *Etlingera* species.
4. Our study demonstrated a high ecological fit between actors of distinct evolutionary history and the general validity of bird-pollination syndrome. We moreover show that trait matching and niche differentiation are important ecological processes also in semi-artificial plant-pollinator systems.

KEYWORDS
bird pollination, co-evolution, convergent evolution, nectarivore, niche differentiation, trait matching

1 | INTRODUCTION

Evolutionary trajectories and related adaptations of ornithophilous plants and nectarivorous birds differ on individual continents and in different phylogenetic plant and bird lineages (Abrahamczyk, 2019; Fleming & Muchhala, 2008). Considering specialized nectarivores, the three largest groups are hummingbirds (Trochilidae) in the New World, sunbirds, and spiderhunters (Nectariniidae) in Africa, Asia, and Australia and honeyeaters (Meliphagidae) in Australia, New Zealand, New Guinea, and many South Pacific islands (Cheke, Mann,

& Allen, 2001; Cronk & Ojeda, 2008; Schuchmann, 1999). Similarly, bird-visited plants can be found in many families. Flores, Ornelas, Wethington, and Arizmendi (2019) reported 105 plant families that contain plant species visited by hummingbirds, 54 of which they classified as ornithophilous or partly ornithophilous. In Australia, Ford, Paton, and Forde (1979) reported 31 plant families visited by birds. In 15 of these families, not only bird-visited but also bird-pollinated species were found. In sunbirds, Cheke et al. (2001) documented the occurrence of food plants in 94 families. For South Africa, Rebelo (1987) reported 30 plant families that contained at least one ornithophilous species.

Many authors have highlighted differences among adaptations in independently evolved bird-pollination systems as well as similarities which are the consequences of convergent evolution. One of the most famous convergent adaptations of specialized nectarivorous birds is thin bills and tubular tongues which enable them to drink nectar from flowers, even though exact bill and tongue parameters differ among individual bird groups (Paton & Collins, 1989). The common flower properties of ornithophilous plants are defined by the bird-pollination syndrome. Bird-pollinated flowers are usually red or orange, without scent and produce a lot of nectar (Cronk & Ojeda, 2008). The most often reported example of specific adaptations is related to the fact that New World hummingbirds usually hover whereas Old World sunbirds perch when feeding (Cronk & Ojeda, 2008; Fleming & Muchhala, 2008; Pyke, 1980). As a consequence, we can find many hummingbird-pollinated plant species which have their flowers oriented into free space in the New World (Westerkamp, 1990) and different plant adaptations which enable perching of passerine birds in the Old World (Frost & Frost, 1981; de Waal, Anderson, & Barrett, 2012). Nevertheless, this dichotomy is not without exceptions and there are known Old World plants adapted to sunbird hovering (Janeček et al., 2011; Janeček, Bartoš, & Njabo, 2015; Padyšáková & Janeček, 2016). Similarly, as demonstrated by the pollination systems of two *Heliconia* spp., foraging behavior, hovering versus perching, can be species-specific in hummingbirds (Taylor & White, 2007). Other discussed differences were assumed to be in nectar properties (Baker, Baker, & Hodges, 1998). Johnson and Nicolson (2008) nevertheless demonstrated that different nectars can be more commonly found among plants visited by specialized versus nonspecialized birds than among plants visited by Old World sunbirds versus New World hummingbirds. For the amount of sucrose in nectar, this specialized versus nonspecialized bird dichotomy was confirmed by Abrahamczyk et al. (2017), who, however, showed that sunbird-pollinated plants have more diverse nectar compositions than hummingbird-pollinated ones.

The differences and similarities discussed above lead to the question: how do different evolutionary trajectories and convergent evolution processes effect the compatibility of individual pollination systems and what is the ecological fit (Janzen, 1985)? In simple terms: can plants be effectively pollinated by birds and can birds feed on plants when they have different evolutionary histories? The answer to this question is important for understanding the consequences of divergent and convergent evolution processes. Moreover, with the recent acceleration of global environmental changes, it can help us to predict scenarios when native partners are lost thanks to biodiversity degradation and/or new invasive partners occur (Cox & Elmqvist, 2000).

The feeding of nectarivorous birds on non-native plants has been reported in America (Maruyama et al., 2016), Asia (Ghadiriani, Qashqaei, & Dadras, 2007), Australia (Ford et al., 1979), and Africa (Geerts & Pauw, 2009a). Records of bird pollination of alien plants are much less common. Sunbirds were recorded as pollinators of invasive tobacco *Nicotiana glauca*, which is naturally pollinated by hummingbirds in America (Ollerton et al., 2012). The sunbirds even pollinate it in a similar way to hummingbirds using hovering flight (Geerts & Pauw, 2009a). Also, in the New World it was shown that the ornamental plant *Strelitzia reginae*, which is native to South Africa, can be pollinated by the local common yellowthroat warbler *Geothlypis trichas* (Hoffmann, Fortier, & Hoffmann-Tsay, 2011). There are, nevertheless, no comparative studies which document how these non-native interactions are affected by evolutionary history and how they function in more complex systems, where other ecological processes, like niche differentiation, might play a role. In our study, we focus on interactions among African sunbirds and alien ornamental plants on a local farm in Cameroon. These farms produce ornamental plants of the spiderhunter-pollinated genus *Etlingera* from Asia (Sakai, Kato, & Inoue, 1999; Sakai, Kawakita, Ooi, & Inoue, 2013) and of the hummingbird-pollinated genus *Heliconia* from America (Linhart, 1973; Temeles & Kress, 2003). Spiderhunters are passerine birds of the genus *Arachnothera*, part of the sunbird family Nectariniidae (Cheke et al., 2001), whereas hummingbirds (family Trochilidae) represent a very distant phylogenetic lineage (Prum et al., 2015). Thus, the farms represent a unique place to study the consequences of specific and convergent adaptations, as well as possible ecological community processes such as niche differentiation. Using this system, we tested the following three scenarios: (a) complete noncompatibility, local sunbirds do not visit any of the plants which evolved on different continents; (b) partial ecological fitting, where birds visit the plants but do not pollinate them (c) full ecological fitting, where birds visit alien plants and pollinate them. Under partial and full ecological fitting scenarios, we expect that sunbirds will show niche differentiation and plants are likely to differ in the spectrum of sunbird visitors. We also decided to determine nectar production and nectar concentration of individual plants to see whether observed patterns can be simply explained by offered rewards.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was performed near Bokwango village (4°8′6″N, 9°13′16″E, 940 m a.s.l.), which is administratively part of Buea town (NW Cameroon). The study site was a local farm where the four target species of genus *Heliconia* and three taxa of genus *Etlingera* are commercially cultivated for flower production, within an area of approximately 1 ha.

2.2 | Plant species

All studied *Heliconia* spp. (Figure 1) are native to Central and/or South America. *H. bihai* (L.) is native in the area from Mexico to Brazil and Peru, it occurs also in the Caribbean. *H. latispatha* Benth. is native from East and South Mexico to NE Peru and Venezuela. *H. rostrata* Ruiz & Pavón is native from Mexico to Amazonian Peru and Ecuador (Andersson, 1981; Berry & Kress, 1991; Govaerts & Kress, 2019) and *H. bihai x caribaea* cv. Jacquinii is native in Grenada. In contrast to the genus *Heliconia*, genus *Etlingera* is native to Indo-Pacific Asia. *Etlingera elatior* (Jack) R.M.Sm. is native in South Thailand, Malaysia, and Indonesia and *Etlingera hemisphaerica* (Blume) R.M.Sm. in Sumatra and Java (Choon & Ding, 2016; Govaerts & Newman, 2019). At the study site, there are two cultivated forms of *E. elatior* which represent the two extremes of the involucral bract color range occurring in nature: the red form with red involucral bracts and white form with whitish-pink involucral bracts (Sabu & Smisha, 2013).

Both *Heliconia* and *Etlingera* spp. produce shoots bearing a maximum of one inflorescence. *Heliconia* spp. produce inflorescences almost always on the leafy shoots and in *Etlingera*, there are special shoots bearing either inflorescence or leaves. The individual flowers of both genera flower for a single day (Berry & Kress, 1991; Choon & Ding, 2016). In *Heliconia*, flowers are usually produced in red and/or yellow inflorescence bracts. Depending on the *Heliconia* species up to 50 flowers can be produced on one bract during the flowering period (Berry & Kress, 1991). Whole inflorescence can be either pendant (Figure 1b) or erect (Figure 1a,c,d). In the *Etlingera* genus, flowers are arranged in dense inflorescence heads containing alternating layers of floral bracts and flowers (Choon & Ding, 2016; Figure 1g–i). In *E. hemisphaerica*, the involucral bracts are red whereas in *E. elatior*, the involucral bracts can range from red (red form) to whitish-pink (grown as white form in our study area) (Sabu & Smisha, 2013).

Most of the *Heliconia* species seem to be self-compatible (Kress, 1983) as was shown also for *H. latispatha* (Kress, 1983) and *H. bihai* (Meléndez-Ackerman, Rojas-Sandoval, & Planas, 2008). Considering the genus *Etlingera*, it was shown that *E. elatior* is self-compatible but self-pollination is much less effective than cross pollination (Sabu & Smisha, 2013).

2.3 | Plant traits

To compare the nectar value of individual species, we measured nectar production over 12 hr. The day before the nectar measurements, we marked flower buds and covered them with dense nets to prevent visitors from consuming the nectar after the flower had opened. If flowers opened on the day of nectar measurement, we marked them again as experimental flowers in the morning (around 6 a.m.). After 12 hr, we collected and measured nectar volume and concentration. Nectar volume was measured by Hamilton syringe (model 702 N) and concentration by pocket refractometer (PAL-1, Atago Co.). Comparison of nectar production was performed on two days, on the 25 and 28 May 2018. The opening of the flowers was sometimes unpredictable and in consequence, we measured in total: 14 flowers on 10 plants of *E. elatior* red form; 11 flowers on 6 plants of *E. elatior* white form, 17 flowers on 10 plants of *E. hemisphaerica*, 9 flowers on 8 plants of *H. bihai*, 10 flowers on 10 plants of *H. bihai x caribaea* cv. Jacquinii; 9 flowers on 9 plants of *H. latispatha*, and 10 flowers on 10 plants of *H. rostrata*.

To compare nectar standing crop (i.e., actual amount of nectar under natural competition), we collected nectar twice per day from five nonmanipulated flowers, each of them on a different flowering shoot. The first harvest was around 10 a.m. and the second around 16 p.m. We measured nectar volume using a Hamilton syringe. Measurement of nectar standing crop was performed on two days 1st and 2nd June. Nevertheless, because of heavy rain on the 1st June in the afternoon, we measured only morning values on this date.

2.4 | Sunbird visitors

Observations of visitors were performed on 11 days between 14 May 2018 and 2 July 2018. During each day, we observed one plant (flowering shoot) of each species. Observation was performed using AEE MagiCam 70S (AEE Technology Co., Ltd) sport cameras. Cameras were permanently connected to power banks. The duration of observations of individual plants on individual days differed due to logistical issues (charging of power banks, downloading data etc.) and some technical errors. In total, each species was observed approximately for 90 hr (Table S1). From the acquired video material, we extracted information on frequencies of visits per inflorescence, per flower and frequency of flower visits when the visitor was in contact with plant reproductive organs.

2.5 | Experiment on sunbird pollination

To assess the significance of sunbirds in plant pollination, we set up a manipulative experiment. In this experiment, we covered randomly selected inflorescences with a sparse net with mesh size of 1 cm to exclude bird visitors. As a control, we marked nonmanipulated inflorescences and allowed them to be naturally exposed to visitors. The day after in the morning, when flowering was over, we collected gynoecia and fixed them in 96% ethanol for future analyses.

In the laboratory, we soaked the gynoecia in distilled water for 24 hr. and then put them into 10 M NaOH for 24 hr. Thereafter, we carefully washed the gynoecia in distilled water and left them overnight in aniline blue dye (Dafni, Kevan, & Husband, 2005). Pollen tubes were counted under a fluorescence microscope. Styles from one inflorescence collected on the same day represented one sample. The experiment took place from 18 till 24 May 2018.

FIGURE 1 Studied plant and bird species. (a) *Cyanomitra oritis* on *Heliconia bihai*, (b) *Heliconia rostrata*, (c) *Heliconia caribaea* x *H. bihai* cv. Jacquinii, (d) and (e) *Cyanomitra olivacea* on *Heliconia latispatha* (f) female of *Cinnyris chloropygius* on *Heliconia latispatha* (g) *Cyanomitra oritis* on *Etlingera elatior* red form (with red invlolucral bracts), (h) *Cyanomitra oritis* on *Etlingera elatior* white form (with whitish-pink involucral bracts), (i) *Cyanomitra oritis* on *Etlingera hemisphaerica*

To test whether there are any problems with pollen tube germination and/or staining (e.g., incompatibility of local pollens, problems with pollen tube coloring etc.), we also set up a hand-pollinated control. In this subexperiment, we supplied stigmas of all species with pollen from distant flowering shoots in the morning. These gynoecia were then processed in the same way as those from the bird exclusion experiment.

2.6 | Statistical analyses

Data from most of the datasets were not normally distributed, and therefore, we used analogical nonparametric permutation methods included in the PERMANOVA program which is an extension of the software PRIMER (Anderson, Gorley, & Clarke, 2008). Data on nectar volumes, visitation frequencies, number of pollen tubes were log (x+1) transformed to decrease the effect of extreme values of dependent variables. In the analyses on differences between genera, we treated species ID nested in Genus and Date (except for analysis on flower length) as random factors. When comparing species, we used Date as a random factor. In analyses on nectar production and concentration, when more samples were taken from one plant, individual plant ID was also treated as a random factor nested in plant species ID.

3 | RESULTS

3.1 | Plant traits

The studied plants differ in total flower length (Figure S1). *Heliconia* spp. have longer flowers than *Etlingera* spp., but this difference was only marginally significant (perm. ANOVA, Genus: $F_{1,63}$ = 7.86, p = .0557). Nevertheless, according to the video analysis the total flower lengths differ from functional lengths, that is terminal parts of flowers are relatively open which allows birds to enter deeper for nectar (the bird's reach is increased beyond the range of its bill and tongue). Flowers of genus *Etlingera* are hidden in compact inflorescences, and birds need to enter the flowers legitimately. In the genus *Heliconia*, flowers are more accessible and birds are able to insert their beak between the not fully united petals and sepals or even pierce the perianth without touching the reproductive organs (Figure 1f, Video S1-3).

Studied plants did not differ in nectar production per flower over 12 hr. (mean = 80.9 μl ± 8.6 SE, Figure 2a; perm. mixed-effect model; Plant Species: $F_{6,39} = 0.96$; $p = .4726$). However, nectar concentration differed between species (Figure 2b; perm. mixed-effect model; Plant Species: $F_{6,39} = 10.99$, $p = .0001$). No significant difference was found between *Heliconia* and *Etlingera* genus in nectar concentration (perm. mixed-effect model; Genus: $F_{1,39} = 0.05$; $p = .8420$). Nectar standing crop differed among species and at different harvest times (morning vs. afternoon), the diurnal changes (interaction) nevertheless did not differ among species (Figure 2c; perm. mixed-effect model; Plant Species: $F_{6,90} = 2.71$, $p = .0202$; Harvest time: $F_{1,90} = 15.29$, $p = .0001$; Interaction Plant Species x Harvest time: $F_{6,90} = 0.26$; $p = .9532$). When considering genera, *Etlingera* had lower standing crops, but this difference was only marginally significant. There was no significant difference between genera in standing crop diurnal changes (perm. mixed-effect model; Genus: $F_{1,95} = 3.14$; $p = .0873$; Harvest time $F_{1,95} = 14.96$; $p = .0002$; Interaction Genera x Harvest time $F_{1,95} = 0.61$; $p = .4331$).

3.2 | Sunbird visitors

Studied plant species were visited by three sunbird species: *Cinnyris chloropygius*, *Cyanomitra olivacea*, and *Cyanomitra oritis*. Although the cameras were set up to record sunbirds (i.e., cameras were as far as possible from the plants to avoid scaring bird visitors, and each inflorescence was recorded from just one side), we also observed some insect visitors. The most common were honeybees but also butterflies and ants were observed on both *Heliconia* and *Etlingera* spp.

The most frequently visited species were *E. elatior* white form (0.94 bird visits flower^{-1} hr^{-1}), *E. hemisphaerica* (0.91), *E. elatior* red form (0.89), and *H. latispatha* with 0.88 bird visits flower^{-1} hr^{-1}. The other three *Heliconia* spp. were visited much less often. *H. bihai* had a visitation frequency of 0.20 bird visits flower^{-1} hr^{-1}, *H. bihai x caribaea* cv. Jacquinii 0.1 visits and *H. rostrata* only 0.07 visits flower^{-1} hr^{-1}.

Both individual plant species and plant genera differed in the spectrum of bird visitors, regardless of whether the frequency of visits per inflorescence or per flower is considered (Table 1). *Etlingera* species were visited mainly by *C. oritis*., *H. latispatha* was visited mainly by *C. chloropygius* followed by *C. olivacea* and *C. oritis*. A much higher frequency of visits to *H. latispatha* was recorded per inflorescence than per flower, and this difference was more obvious than for *Etlingera* species (Figure 3a,b). When we tested the opposite, that is how bird species differed in the spectrum of visited plants, there were significant differences between bird species when considering frequency of visits per inflorescence but only a marginally significant difference when considering frequency per flower (Table 1; Figure S2).

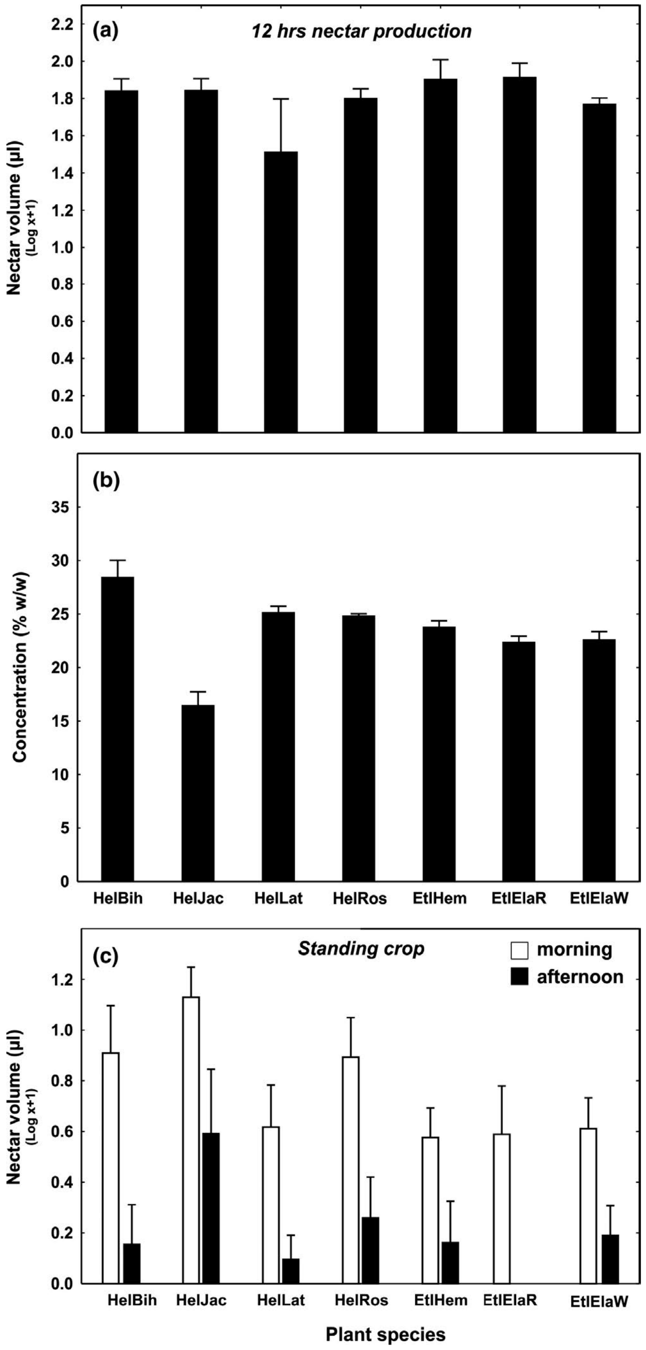

FIGURE 2 Nectar properties of studied plants. (a) 12 hr. nectar production in covered flowers, (b) concentration of nectar, (c) nectar standing crop in nonmanipulated flowers. *HelBih*, *Heliconia bihai*; *HelJac*, *Heliconia bihai* x *H.caribea* ("Jacquinii"); *HelLat*, *Heliconia latispatha*; *HelRos*, *Heliconia rostrata*; *EtlHem*, *Etlingera hemisphaerica*; *EtlElaR*, *Etlingera elatior* red form; *EtlElaW*, *Etlingera elatior* white form. Means plus SE are shown

TABLE 1 PERMANOVA analyses on differences between visitor communities on plant species (i.e., plant species as an explanatory variable), differences in visitor communities between genera (i.e., plant genera as an explanatory variable), and differences in the spectrum of plants visited by individual bird species (i.e., bird species as an explanatory variable) and comparing visitation community on individual plant species (i.e., plant species as an explanatory variable). Data were log (x+1) transformed. Date was used as a random effect in all analyses. In addition, to test the effect of genus we considered plant species nested in factor genus as a random factor

	Plant species		Plant genera		Bird species	
	F_{ps}	p	F_{ps}	p	F_{ps}	p
Frequency of visits per inflorescence	4.50	.0001	3.35	.0284	3.12	.0293
Frequency of visits per flower	3.31	.0005	8.36	.0278	2.81	.0601
Frequency of touching reproductive organs	2.73	.0071	25.26	.0287	2.68	.0720

When considering sunbird pollination potential (expressed as frequency of contacts with reproductive organs), sunbird pollination communities of individual plants and genera differed (Table 1; Figure 3c). Contact with reproductive organs was detected, due to the structure of flowers, during all visits on *Etlingera* species (Figure 1g) and the beaks of sunbirds were often densely covered with sticky pollen grains (Figure 1i; Video S3). In contrast, on the most often visited *Heliconia*, *H. latispatha*, sunbirds frequently drank nectar without touching the reproductive organs (Figure 1f; Video S1). In *H. latispatha*, 16.6% of flower visits of *C. chloropygius*, 89.2% visits of *C. olivacea*, and 39.5% visits of *C. oritis* involved contact with reproductive organs. The analysis of the opposite scenario (i.e., if individual bird species differ in the spectrum of plant species of which they were in contact with reproductive organs) showed only marginally significant results (Table 1; Figure S2c).

3.3 | Experiment on sunbird pollination

After a controlled hand pollination supplement, we observed germinating pollen grains on the stigmas of *Etlingera* spp. (Figure 4c). In contrast, almost no germinating pollen grains were observed on the stigmas of *Heliconia* spp. (Figure S3). The same pattern was observed in the experiment (Figure 4). Pollen tubes on *Heliconia* plants moreover germinated on the stigma and did not grow into the style (Figure 4b). Plant species differed in pollen tube number, sunbird exclusion had a negative effect on the number of pollen tubes, and this treatment was species-specific (perm. mixed-effect model; Plant: $F_{6,334}$ = 11.81, p = .0001; Treatment: $F_{1,334}$ = 6.90, p = .0092; Plant x Treatment $F_{6,334}$, p = .0020). Genera differed in the number of pollen tubes and were differently affected by the treatment (perm. mixed-effect model; Genus: $F_{1,339}$ = 4.61, p = .0292; Treatment: $F_{1,339}$ = 9.46; Genus x Treatment $F_{1,339}$ = 12.43; p = .0006).

4 | DISCUSSION

Our study demonstrated a high degree of ecological fitting. We also show that distant evolutionary history of individual actors cannot prevent fundamental ecological processes such as occupation of new niches by alien plants or niche partitioning.

Our study complements the ideas of Janzen (1985) that most of the interactions we see around us are not necessarily the consequences of coevolutionary processes in a given place, but of simple ecological fitting. Janzen´s main arguments were that biological communities are dominated by widespread invasive species, which have extended their range and are not originally adapted to most of their habitats. From this point of view, our study can be considered experimental support of this statement showing that organisms from three different continents can create a complex interacting community on the basis of ecological fitting.

However, we have also shown that the Asian *Etlingera* spp. established tighter interactions with African sunbirds. *Etlingera* spp. were visited legitimately more often, and sunbirds seem to be very effective pollinators. From the sunbirds' point of view, it does not seem to be a simple consequence of bigger rewards, because both *Etlingera* and *Heliconia* spp. produced similar amounts of nectar. *Etlingera* spp. even had a slightly lower nectar standing crop (but only marginally significant). We assume the reason for this perfect ecological fit could be a more comfortable perching position when feeding and from the plant's point of view, the compact inflorescence enables only legitimate entering of the flowers. Pollen of *Etlingera* spp. is then precisely placed in high quantity on the bills of perching sunbirds. *Heliconia* spp. had weaker but still functional interactions with the local sunbirds which is amazing if we consider that the genus *Heliconia* is in the oldest known clade of hummingbird-pollinated plants (Iles et al., 2017). We were surprised how *H. rostrata*, which is pollinated by hovering hummingbirds (Iles et al., 2017), is able to precisely place pollen on the heads of perching *C. olivacea* and *C. oritis* (Video S2). *Heliconia* spp. were not visited with the same frequency indicating that also intragenus trait differences are important. We assume that the high visitation rate of *H. latispatha* is mainly due to fact that the flowers are not deeply hidden in bracts and can be more easily reached in both legitimate and illegitimate ways. Although we observed frequent contacts of *Heliconia* reproductive organs and even pollen on the heads of sunbirds, we were not able to evaluate pollinator effectivity directly by counting germinated pollen tubes. There were almost no pollen tubes observed, or they did not grow inside the style. Because this was the case not only for experimental treatments but also for hand pollination, we

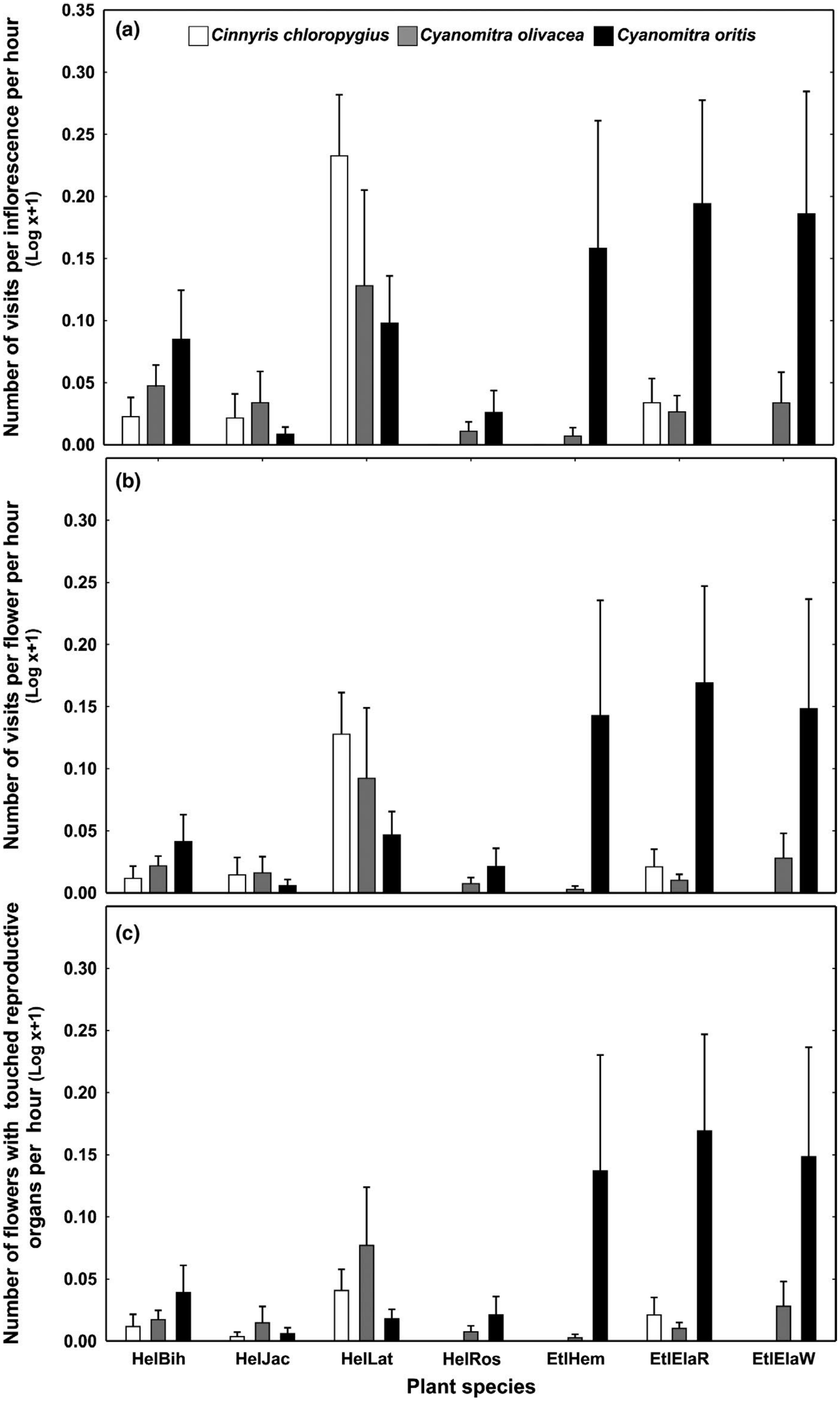

FIGURE 3 Frequencies of visits on (a) inflorescences, (b) flowers, and (c) flowers when reproductive organs were touched. For plant abbreviations, see Figure 2. Means plus SE are shown

cannot presume that this was the consequence of pollinator infectivity in pollen transport. In consequence, we can only speculate whether this was caused by intraspecific pollen transport or by high inbreeding depression because of low genetic diversity on the farms where plants are propagated only clonally. Although we optimized the staining technique over a long time period and followed experimental methods of other researchers working on *Heliconia* pollen tubes (Betts, Hadley, & Kress, 2015), it is possible that these negative results are the consequence of a methodological mistake. This can be supported by the fact that *Heliconias* on the farm produced fruits (including *H. rostrata* of which we did not observed any pollen tubes).

On the plantation, we also observed niche differentiation among individual plant and bird species. *Etlingera* spp., which are adapted to long-billed spiderhunters in Asia (Sakai et al., 1999; 2013), were visited in the new habitat by long-billed sunbirds *C. oritis*. The medium bill-sized sunbird *C. olivacea* visited mainly *H. latispatha* with more reachable nectar but also fed on *Etlingera* spp. The short-billed

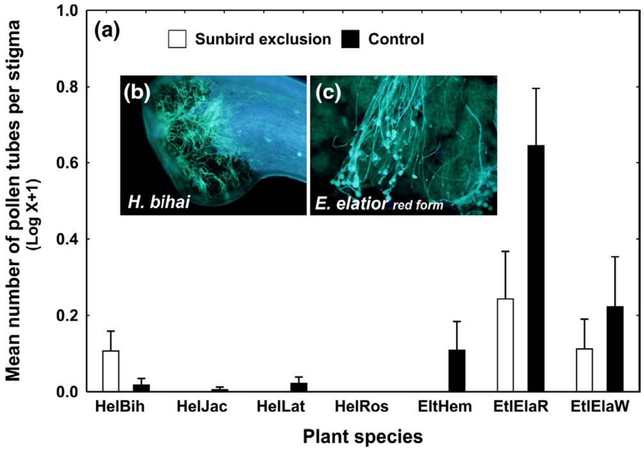

FIGURE 4 (a) Results of experimental exclusion of sunbirds. Germinating pollen grains on stigma of *Heliconia bihai* (b) and *Etlingera elatior* (c). For plant abbreviations, see Figure 2. Means plus SE are shown

C. chloropygius visited mainly *H. latispatha* where it, however, mainly thieved nectar. *H. bihai*, which has flowers more hidden in the bracts, was mostly visited by long-billed *C. oritis*. This type of niche differentiation based on bill length was described for two *Heliconia* and three hummingbird species in Costa Rica by Taylor and White (2007), but we can find it also in others natural communities both in the New (Feinsinger, Swarm, & Wolfe, 1985) and Old World (Ford & Paton, 1977; Geerts & Pauw, 2009b; Janeček et al., 2012). The thieving behavior of short-billed birds on long tubular flowers, as observed mainly for *H. latispatha*–*C. chloropygius* interaction, is common in natural pollination systems. This behavior was shown for sunbirds (Geerts & Pauw, 2009b; Janeček et al., 2015) as well as for hummingbirds (Gill, 1987; Maglianesi, Blüthgen, Gaese, & Schleuning, 2014; Maruyama, Bugoni, Dalsgaard, Sazima, & Sazima, 2015).

Using this example of a semiarbitrary plant–bird community from three continents, we demonstrated that potential ornithophilous invasive plants can be easily incorporated into local communities. In consequence, we are delivering a similar message from Africa as Maruyama et al. (2016) from America. Sunbird pollination networks and hummingbird networks are open to exotic plant species. Nevertheless, it is a question to which degree this is a worrying message. From the birds' point of view, local flower farms represent a rich nectar source. During our research on Mt. Cameroon, we never observed such a high density of sunbirds anywhere else in the region. For example, at the plantation with ornamental flowers we caught 62 individuals of the endemic sunbird *C. oritis* during three days of extensive mist-netting, whereas at a congruent elevation in natural forest on Mt. Cameroon, we only caught 15 individuals of *C. oritis* despite a comparable amount of sampling effort. The effect on local flora can nevertheless be much more controversial. It was demonstrated that alien plants have a negative effect on both visitation and reproductive success of native coflowering species (Morales & Traveset, 2009). In consequence, the effects of these plantations on local flora need to be studied in detail.

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AUTHOR CONTRIBUTIONS

ŠJ conceived the ideas and designed methodology. Fieldwork and laboratory work was conducted by ŠJ, KC, GU, PJ, EC, ZS, and FLE. ŠJ analyzed the data. ŠJ led the writing of the manuscript. All authors contributed critically to the drafts and gave approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.qnk98sfbx

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REFERENCES

Abrahamczyk, S. (2019). Comparison of the ecology and evolution of plants with a generalist bird pollination system between continents and islands worldwide. *Biological Reviews*, *94*(5), 1658–1671. https://doi.org/10.1111/brv.12520

Abrahamczyk, S., Kessler, M., Hanley, D., Karger, D. N., Müller, M. P. J., Knauer, A. C., … Humphreys, A. M. (2017). Pollination adaptation and the evolution of floral nectar sugar composition. *Journal of Evolutionary Biology*, *30*, 112–127. https://doi.org/10.1111/jeb.12991

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). *PERMANOVA+ for PRIMER: Guide to software and statistical methods*. Plymouth: PRIMER-E.

Andersson, L. (1981). Revision of *Heliconia* sect. Heliconia (Musaceae). *Nordic Journal of Botany*, *1*, 759–784. https://doi.org/10.1111/j.1756-1051.1981.tb01163.x

Baker, H. G., Baker, I., & Hodges, S. A. (1998). Sugar composition of nectars and fruits consumed by birds and bats in the tropics and subtropics. *Biotropica*, *30*, 559–586. https://doi.org/10.1111/j.1744-7429.1998.tb00097.x

Berry, F., & Kress, W. J. (1991). *Heliconia an identification guide*. Washington, DC: Smithsonian Institution Press.

Betts, M. G., Hadley, A. S., & Kress, W. J. (2015). Pollinator recognition by a keystone tropical plant. *Proceedings of the National Academy of Sciences United States of America*, *112*, 3433–3438. https://doi.org/10.1073/pnas.1419522112

Cheke, R. A., Mann, C. F., & Allen, R. (2001). *Sunbirds, a guide to the sunbirds, flowerpeckers, spiderhunters and sugarbirds of the world*. London: Christopher Helm.

Choon, S. Y., & Ding, P. (2016). Growth stages of torch ginger (*Etlingera elatior*) plant. *Sains Malaysiana*, *45*, 507–515.

Cox, P. A., & Elmqvist, T. (2000). Pollinator extinction in the Pacific Islands. *Conservation Biology*, *14*, 1237–1239. https://doi.org/10.1046/j.1523-1739.2000.00017.x

Cronk, Q., & Ojeda, I. (2008). Bird-pollinated flowers in an evolutionary and molecular context. *Journal of Experimental Botany*, *59*, 715–727. https://doi.org/10.1093/jxb/ern009

Dafni, A., Kevan, P. G., & Husband, B. C. (2005). *Practical pollination biology*. Cambridge, Ontario: Enviroquest Ltd.

de Waal, C., Anderson, B., & Barrett, S. C. H. (2012). The natural history of pollination and mating in bird-pollinated *Babiana* (Iridaceae). *Annals of Botany*, *109*, 667–679. https://doi.org/10.1093/aob/mcr172

Feinsinger, P., Swarm, L. A., & Wolfe, J. A. (1985). Nectar-feeding birds on Trinidad and Tobago: Comparison of diverse and depauperate guilds. *Ecological Monographs*, *55*, 1–28. https://doi.org/10.2307/1942523

Fleming, T. H., & Muchhala, N. (2008). Nectar feeding bird and bat niches in two worlds: Pantropical comparisons of vertebrate pollination systems. *Journal of Biogeography*, *35*, 764–780. https://doi.org/10.1111/j.1365-2699.2007.01833.x

Flores, C. I. R., Ornelas, J. F., Wethington, S., & Arizmendi, M. D. C. (2019). Are hummingbirds generalists or specialists? Using network analysis to explore the mechanisms influencing their interaction with nectar resources. *PLoS ONE*, *14*, e0211855. https://doi.org/10.1371/journal.pone.0211855

Ford, H. A., & Paton, D. C. (1977). The comparative ecology of ten species of honeyeaters in South Australia. *Australian Journal of Ecology*, *2*, 399–407. https://doi.org/10.1111/j.1442-9993.1977.tb01155.x

Ford, H. A., Paton, D. C., & Forde, N. (1979). Birds as pollinators of Australian plants. *New Zealand Journal of Botany*, *17*, 509–519. https://doi.org/10.1080/0028825X.1979.10432566

Frost, S. K., & Frost, P. G. H. (1981). Sunbird pollination of *Strelitzia nicolai*. *Oecologia*, *49*, 379–384. https://doi.org/10.1007/BF00347603

Geerts, S., & Pauw, A. (2009a). African sunbirds hover to pollinate an invasive hummingbird-pollinated plant. *Oikos*, *118*, 573–579. https://doi.org/10.1111/j.1600-0706.2008.17167.x

Geerts, S., & Pauw, A. (2009b). Hyper-specialization for long-billed bird pollination in a guild of South African plants: The Malachite Sunbird pollination syndrome. *South African Journal of Botany*, *75*, 699–706. https://doi.org/10.1016/j.sajb.2009.08.001

Ghadiriani, T., Qashqaei, A. T., & Dadras, M. (2007). Notes on feeding and breeding habits of the purple sunbird *Nectarinia asiatica* (*Cinnyris asiaticus*) in Bandar Abbas, Hormozgan, Southern Iran. *Podoces*, *2*, 122–126.

Gill, F. B. (1987). Ecological fitting: Use of floral nectar in *Heliconia stilesii* Daniels by three species of Hermit hummingbirds. *The Condor*, *89*, 779–787. https://doi.org/10.2307/1368525

Govaerts, R., & Kress, J. (2019). World checklist of Heliconiaceae. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. Retrieved from http://wcsp.science.kew.org/

Govaerts, R., & Newman, M. (2019). World Checklist of Zingiberaceae. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. Retrieved from http://wcsp.science.kew.org/

Hoffman, F., Fortier, F. D. A., & Hoffmann-Tsay, S. S. (2011). Efficient avian pollination on *Strelitzia reginae* outside of South Africa. *South African Journal of Botany*, *77*, 503–505. https://doi.org/10.1016/j.sajb.2010.09.018

Iles, W. J. D., Sass, C., Lagomarsino, L., Benson-Martin, G., Driscoll, H., & Specht, C. D. (2017). The phylogeny of *Heliconia* (*Heliconiaceae*) and the evolution of floral presentation. *Molecular Phylogenetics and Evolution*, *117*, 150–167. https://doi.org/10.1016/j.ympev.2016.12.001

Janeček, Š., Bartoš, M., & Njabo, K. Y. (2015). Convergent evolution of sunbird pollination systems of Impatiens species in tropical Africa and hummingbird systems of the New World. *Biological Journal of the Linnean Society*, *115*, 127–133. https://doi.org/10.1111/bij.12475

Janeček, Š., Patáčová, E., Bartoš, M., Padyšáková, E., Špitzer, L., & Tropek, R. (2011). Hovering sunbirds in the Old World: Occasional behaviour or evolutionary trend? *Oikos*, *120*, 178–183. https://doi.org/10.1111/j.1600-0706.2010.18612.x

Janeček, Š., Riegert, J., Bartoš, M., Hořák, D., Reif, J., Padyšáková, E., … Doležal, J. (2012). Food selection by avian floral visitors: An important aspect of plant-flower interactions in West Africa. *Biological Journal of the Linnean Society*, *107*, 355–367. https://doi.org/10.1111/j.1095-8312.2012.01943.x

Janzen, D. H. (1985). On ecological fitting. *Oikos*, *45*, 308–310. https://doi.org/10.2307/3565565

Johnson, S. D., & Nicolson, S. W. (2008). Evolutionary associations between nectar properties and specificity in bird pollination systems. *Biological Letters*, *4*, 49–52. https://doi.org/10.1098/rsbl.2007.0496

Kress, W. J. (1983). Self-incompatibility in central American *Heliconia*. *Evolution*, *37*, 735–744. https://doi.org/10.1111/j.1558-5646.1983.tb05595.x

Linhart, Y. B. (1973). Ecological and behavioral determinants of pollen dispersal in hummingbird-pollinated *Heliconia*. *The American Naturalist*, *107*, 511–523. https://doi.org/10.1086/282854

Maglianesi, M. A., Blüthgen, N., Gaese, K. B., & Schleuning, M. (2014). Morphological traits determine specialization and resource use in plant-hummingbird networks in the neotropics. *Ecology*, *95*, 3325–3334. https://doi.org/10.1890/13-2261.1

Maruyama, P. K., Bugoni, J. V., Dalsgaard, B., Sazima, I., & Sazima, M. (2015). Nectar robbery by hermit hummingbird: Association to floral phenotype and its influence on flowers and network structure. *Oecologia*, *178*, 783–793. https://doi.org/10.1007/s00442-015-3275-9

Maruyama, P. K., Vizentin-Bugoni, J., Sonne, J., Martín González, A. M., Schleuning, M., Araujo, A. C., … Dalsgaard, B. O. (2016). The integration of alien plants in mutualistic plant-hummingbird networks across the Americas: The importance of species traits and insularity. *Diversity and Distributions*, *22*, 672–681. https://doi.org/10.1111/ddi.12434

Meléndez-Ackerman, E., Rojas-Sandoval, J., & Planas, S. (2008). Self-compatibility of microgametophytes in *Heliconia bihai* (Heliconiaceae) from St. Lucia. *Caribbean Journal of Science*, *44*, 145–149. https://doi.org/10.18475/cjos.v44i2.a3

Morales, C. L., & Travest, A. (2009). A meta-analysis of impact of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, *12*, 716–728. https://doi.org/10.1111/j.1461-0248.2009.01319.x

Ollerton, J., Watts, S., Connerty, S., Lock, J., Parker, L., Wilson, I., … Stout, J. C. (2012). Pollination ecology of the invasive tree tobacco *Nicotiana glauca*: Comparisons across native and non-native ranges. *Journal of Pollination Ecology*, *9*, 85–95. https://doi.org/10.26786/1920-7603(2012)12

Padyšáková, E., & Janeček, Š. (2016). Sunbird hovering behavior is determined by both the forager and resource plant. *Biotropica*, *48*, 687–693. https://doi.org/10.1111/btp.12345

Paton, D. C., & Collins, B. G. (1989). Bills and tongues of nectar-feeding birds: A review of morphology, function and performance, with intercontinental comparisons. *Australian Journal of Ecology*, *14*, 473–506. https://doi.org/10.1111/j.1442-9993.1989.tb01457.x

Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M., & Lemmon, A. R. (2015). A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, *526*, 569–573. https://doi.org/10.5281/zenodo.28343

Pyke, G. H. (1980). The foraging behaviour of Australian honeyeaters: A review and some comparisions with hummingbirds. *Australian Journal of Ecology*, *5*, 343–369. https://doi.org/10.1111/j.1442-9993.1980.tb01258.x

Rebelo, A. G. (1987). A preliminary synthesis of pollination biology in the Cape flora. South African National Scientific Programmes Report 141. Pretoria: CSIR.

Sabu, A. K. M., & Smisha, K. P. (2013). Reproductive biology of *Etlingera elatior* (Jack.) R. M. SM. ornamental torch ginger. *International Journal of Plant, Animal and Environmental Science*, *3*, 75–80.

Sakai, S., Kato, M., & Inoue, T. (1999). Three pollination guilds and variation in floral characteristics of Bornean gingers (Zingiberaceae and Costaceae). *American Journal of Botany*, *86*, 646–658. https://doi.org/10.2307/2656573

Sakai, S., Kawakita, A., Ooi, K., & Inoue, T. (2013). Variation in the strength of association among pollination systems and floral traits: Evolutionary changes in the floral traits of Bornean gingers (Zingiberaceae). *American Journal of Botany*, *100*, 546–555. https://doi.org/10.3732/ajb.1200359

Schuchmann, K. L. (1999). Family Trochilidae (hummingbirds). In: D. J. Hoyo, A. Elliott, & J. Sargatal (Eds.), *Handbook of the birds of the World* (pp. 468–680). Vol. *5*. Barcelona: Lynx Editions.

Taylor, J., & White, S. A. (2007). Observation of hummingbird feeding behavior at flowers of *Heliconia beckneri* and *H. tortuosa* in southern Costa Rica. *Ornitologia Neotropical*, *18*, 133–138.

Temeles, E. J., & Kress, W. J. (2003). Adaptation in a plant-hummingbird association. *Science*, *300*, 630–633. https://doi.org/10.1126/science.1080003

Westerkamp, C. (1990). Bird-flowers, hovering versus perching exploitation. *Botanica Acta*, *103*, 366–371. https://doi.org/10.1111/j.1438-8677.1990.tb00176.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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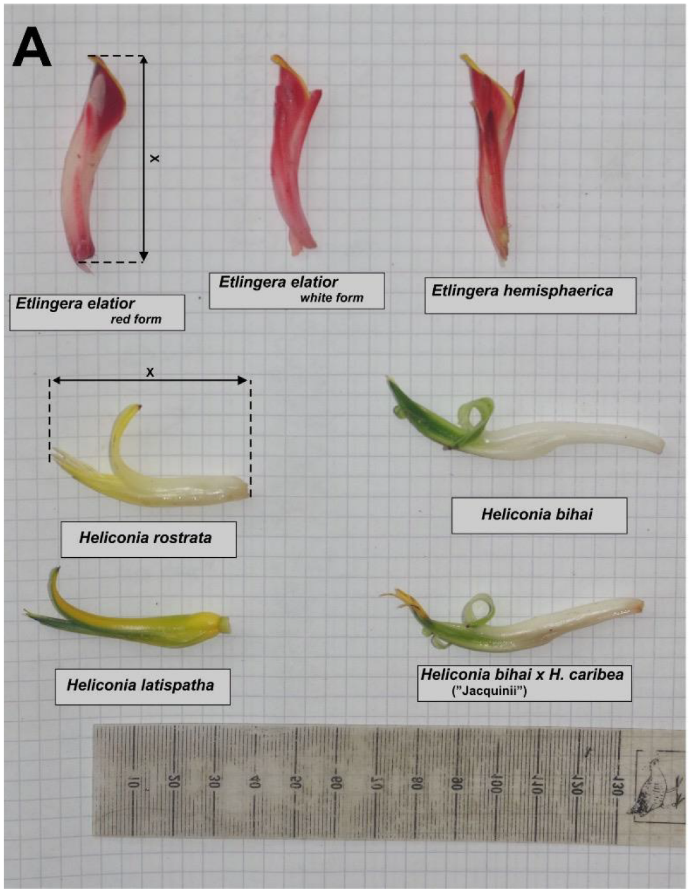
SUPPORTING INFORMATION CHAPTER II

Janeček, Š., Chmel, K., **Uceda Gómez, G.**, Janečková, P., Chmelová, E., Sejfová, S., & Ewome, F.L. (2020). Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution*, 10, 1784–1793. https://doi.org/10.1002/ece3.5942

Table S1. Sampling effort. Duration of observations of individual plants (hours). ***HelBih*** - *Heliconia bihai*, ***HelJac*** = *Heliconia bihai* x *H.caribea* ("Jacquinii"), ***HelLat*** - *Heliconia latispatha* , ***HelRos*** - *Heliconia rostrata*, ***EtlHem*** - *Etlingera hemisphaerica*, ***EtlElaR*** - *Etlingera elatior* red form, ***EtlElaW*** - *Etlingera elatior* white form

Plant No.	**HelBih**	**HelJac**	**HelLat**	**HelRos**	**EtlHem**	**EtlElaR**	**EtlElaW**
1	5.5	5.5	5.6	5.7	5.4	5.2	4.7
2	6.4	5.5	5.5	5.5	6.6	5.2	4.7
3	11.5	10.5	11.7	12	11	9.6	11.8
4	5.5	5.9	10.4	5.3	5.8	6	5.8
5	8.6	7.3	10.4	10.9	9.1	10.5	10.7
6	10.4	10.4	10.6	10.5	9.3	10.6	10.4
7	10.1	10.7	10.2	10.3	10.4	10.5	9.1
8	6.5	7	7.1	6.9	7	6.9	2.3
9	6.2	7.8	6.1	5.7	6.2	5.9	6.1
10	10.5	1.9	10.7	10.2	10.5	10.2	10.8
11	10.6	8.5	10.6	10.2	10.4	9.2	10.8
TOTAL	**91.8**	**81**	**98.9**	**93.2**	**91.7**	**89.8**	**87.2**



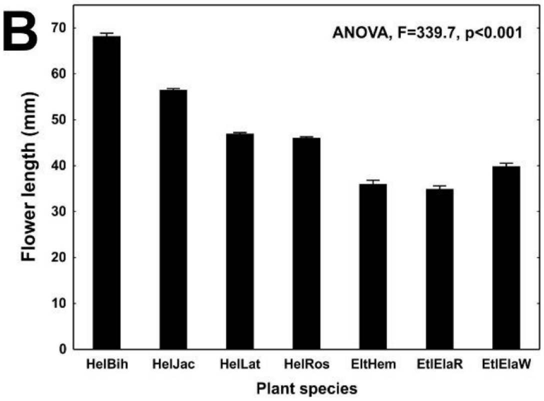


Figure S1: A/ Flowers of studied species. distance ***x*** indicates measured flower lengths. **B/** Flower lengths of individual plant species. ***HelBih*** - *Heliconia bihai*, ***HelJac*** = *Heliconia bihai x H.caribea* ("Jacquinii"), ***HelLat*** - *Heliconia latispatha* , ***HelRos*** - *Heliconia rostrata*, ***EtlHem*** - *Etlingera hemisphaerica,* ***EtlElaR*** - *Etlingera elatior* red form, ***EtlElaW*** - *Etlingera elatior* white form. 10 flowers, each from different speciment, were measured for each species, mean + SE are shown.

Figure S1

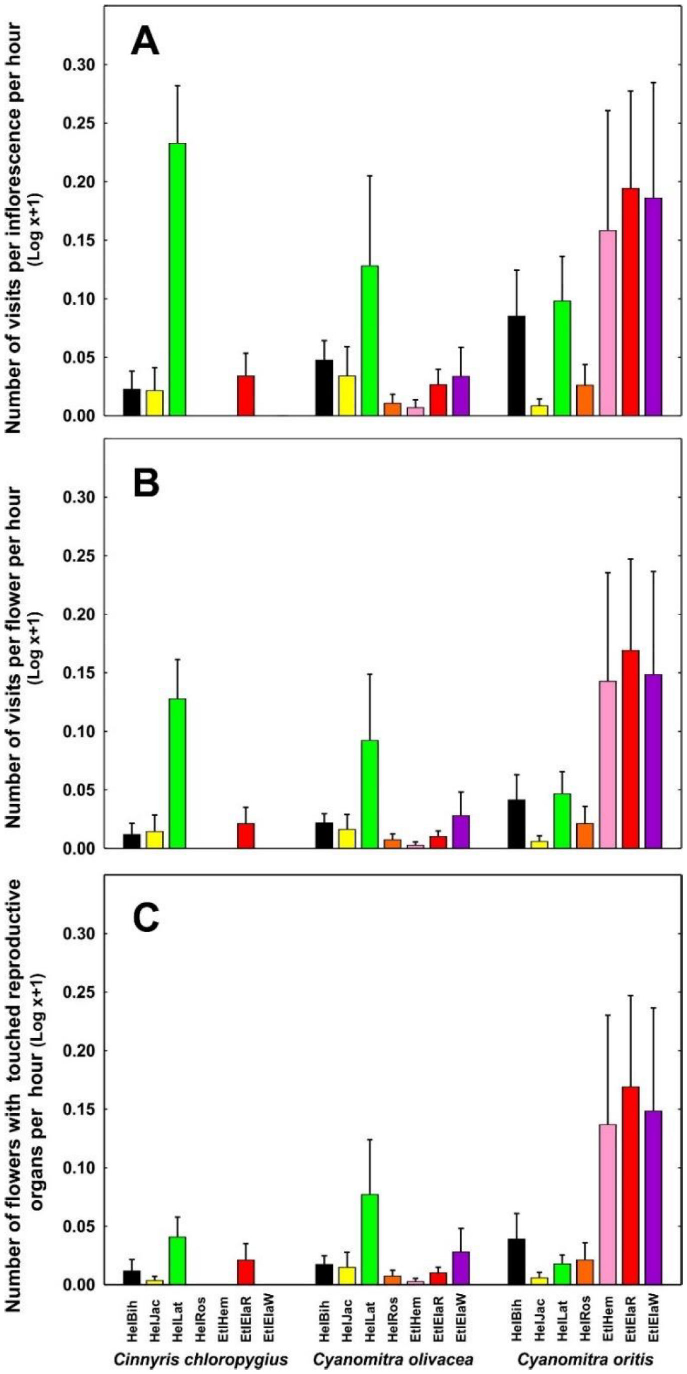


Figure S2: Frequencies of visits on **A/** inflorescences, **B/** flowers and **C/** flowers with touched reproductive organs. ***HelBih*** - *Heliconia bihai*, ***HelJac*** = *Heliconia bihai* x *H.caribea* (”Jacquinii”), ***HelLat*** - *Heliconia latispatha* , ***HelRos*** - *Heliconia rostrata*, ***EtlHem*** - *Etlingera hemisphaerica*, ***EtlElaR*** - *Etlingera elatior* red form, ***EtlElaW*** - *Etlingera elatior* white form. Means plus SE are shown.

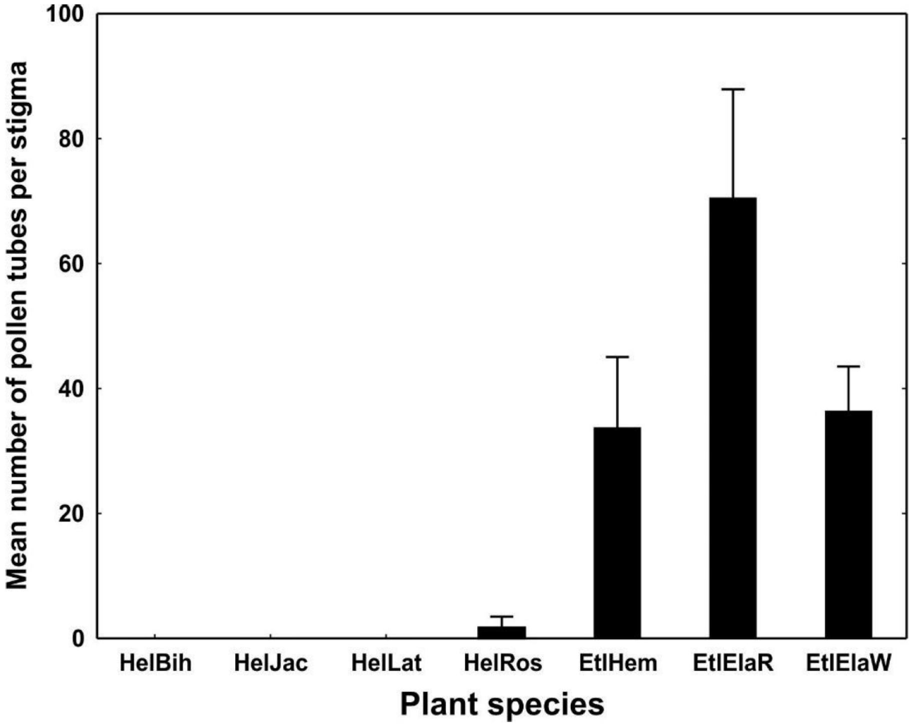


Figure S3: Hand pollination of studied plants. ***HelBih*** - *Heliconia bihai*, ***HelJac*** = *Heliconia bihai* x *H.caribea* (”Jacquinii”), ***HelLat*** - *Heliconia latispatha* , ***HelRos*** - *Heliconia rostrata*, ***EtlHem*** - *Etlingera hemisphaerica*, ***EtlElaR*** - *Etlingera elatior* red form, ***EtlElaW*** - *Etlingera elatior* white form. Means plus SE are shown.

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The ornithophily of *Impatiens sakeriana* does not guarantee a preference by sunbirds

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In recent decades, the tight mutual specialization between nectarivorous birds and ornithophilous plants has been questioned, and instead, high degrees of generalization and interaction asymmetry have been highlighted. Here, we studied interactions among two sunbirds and four plant species in two Mount Cameroon forests, with two plant species from each forest. First, we investigated whether sunbirds differ in frequencies of visitation to target plant species in natural conditions. Second, using a cage experiment, we investigated whether sunbirds prefer various plant species, plants with which they are more familiar and that occur in the habitat where they were caught and/or the only studied ornithophilous plant, *Impatiens sakeriana*. In natural conditions, the short-billed sunbird, *Cinnyris reichenowi*, fed more on flowers with shorter tubes than the long-billed sunbird, *Cyanomitra oritis*. Likewise, sunbirds differed in their experimental preferences. Local plants were generally preferred. This was most obvious in the case of *I. sakeriana*, which was often visited by both sunbirds, but only in the habitat where it grows naturally. This study supports the importance of associative learning. Together with other studies, we suggest that the signalling traits of flowers with bird pollination syndromes evolved to filter out other visitors rather than to attract bird pollinators.

ADDITIONAL KEYWORDS: bird preferences – Cameroon – nectar – niche differentiation – ornithophily.

INTRODUCTION

The relationships between pollinators and plants have fascinated scientists for centuries (Waser, 2006). Despite a long period of research, our understanding of these relationships has changed considerably in the last few decades. The primary ideas on the evolution of plant–pollinator interactions were based on Darwin's co-evolutionary race principle (Darwin, 1862), whereby adaptations by one of the interacting partners impose selection pressure on the other partner, making the relationship between the partners more ecologically specialized. Perhaps the most popular example of these ideas is pollination of the long-spurred orchid *Angraecum sesquipedale* by the long-proboscis moth *Xanthopan morgani*, the moth species whose existence was predicted by Darwin (1862) and later discovered by Rothschild (1903). Nevertheless, in contrast to these original ideas, it was recently demonstrated that: (1) pollination systems are usually more generalized (Waser *et al.*, 1998); (2) not only pollinators, but also other biotic and/or abiotic factors shape the evolution of flower traits (Wang *et al.*, 2013; Ehrlén, 2015); (3) instead of reciprocal co-adaptation, plant phylogenetic lineages often adapted to already preadapted pollinators (Whittall & Hodges, 2007; Ramírez *et al.*, 2011; Abrahamczyk *et al.*, 2017); (4) pollination syndromes (i.e. the sets of floral traits representing adaptations to one pollinator group) are not often good predictors of the real pollinators (Ollerton *et al.*, 2009; Klomberg *et al.*, 2022); and (5) plant–pollinator interactions can be highly asymmetric (Vázquez & Aizen, 2004).

Some of the most commonly studied plant–pollinator interactions are those between nectarivorous birds and ornithophilous plants. The reciprocal benefits in these interactions are driven by both plant and bird adaptations. Ornithophilous plants are often

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*Corresponding author. E-mail: janecek.stepan@centrum.cz distinguished by a set of floral traits known as a bird pollination syndrome. Flowers with a bird pollination syndrome are typically orange or red, without nectar guides. They produce a large volume of nectar with a medium concentration, which accumulates in long floral tubes (Faegri & van der Pijl, 1979; Fenster *et al.*, 2004, 2015; Cronk & Ojeda, 2008; for details and discussion on less specialized brush flowers, see Stiles, 1981). The flowers are also characterized by having no scent or minimal scent as perceived by humans, although this does not mean that they do not produce any volatile compounds (Knudsen *et al.*, 2004) or that nectarivorous birds have no sense of smell (Goldsmith & Goldsmith, 1982). Additionally, nectarivorous birds have many adaptations for feeding on nectar. Examples of such adaptations include a low body weight, a slender bill, a tongue with the ability to take up nectar and the ability to reach flowers by hovering in flight (Stiles, 1981; Westerkamp, 1990; Wester, 2014).

Despite these adaptations, it seems that these relationships are not as close as one would expect. It was demonstrated that birds not only feed on specialized plants but also visit flowers with other pollination syndromes. Frequent feeding on non-specialized plants pollinated by insects was demonstrated even for the two most morphologically specialized nectarivorous bird groups [i.e. hummingbirds (Araujo & Sazima, 2003; Maruyama *et al.*, 2013) and sunbirds (Janeček *et al.*, 2012; Padyšáková *et al.*, 2013; Nsor *et al.*, 2019; Chmel *et al.*, 2021)]. Likewise, plants bearing bird pollination syndromes can be pollinated by insects (Pleasants & Waser, 1985; Mayfield *et al.*, 2001; Schmid *et al.*, 2011).

The coexistence of nectarivorous birds in local communities is often explained by niche (resource) partitioning based on plant and bird traits (Snow & Snow, 1972; Janeček *et al.*, 2012). This partitioning can either result from forbidden interactions (e.g. situations in which some bird species do not visit particular plants at all, given the absence of phenological overlap or morphological mismatch; Vizentin-Bugoni *et al.*, 2014) or result from different competitive abilities on flowers of individual plant species (i.e. if some bird species are less effective in harvesting nectar from flowers than others; Janeček *et al.*, 2012; Janečková *et al.*, 2020). It is widely believed that short-billed hummingbirds drink from wider flowers with short petals and that hummingbirds with longer bills have close interactions with flowers bearing long, narrow corollas. However, most of the time, long-billed species have access to both short and long flowers. Despite this, they do not often visit short flowers, where they need to compete with short-billed species (Bergamo *et al.*, 2017). Furthermore, birds with curved bills will forage on straight-petalled flowers, but straight-billed birds are less likely to visit curved flowers (Maglianesi *et al.*, 2014). Hart & Hunt (2007) stated that birds have red photoreceptors and are attuned to red colours, among the most typical traits of flowers with bird pollination syndromes. Nevertheless, experiments have demonstrated that hummingbirds do not prefer red feeders, instead visiting feeders of various colours (Sherman, 1913; Bené, 1941; Collias & Collias, 1968; Miller & Miller, 1971). The feeder experiments also revealed that for hummingbirds, the association between colour and offered reward is more important than the colour itself (Goldsmith & Goldsmith, 1979). Moreover, the association of a high-quality reward with feeder position seems to be stronger than the association with colour (Collias & Collias, 1968; Miller & Miller, 1971). The switch to other feeder positions and/or colours is preceded by occasional exploration (Collias & Collias, 1968). An alternative hypothesis suggests that a red colour can be the signal that hummingbirds learn and use when entering a new feeding territory and/or facilitates their feeding during migrations (Grant, 1966). Nevertheless, even plant–sunbird interactions, which at first seem to be highly specialized, do not need to be the result of joint co-evolution; they might simply be a consequence of ecological fitting (Janeček *et al.*, 2020).

In this study, we investigated experimentally the preferences of sunbirds for the ornithophilous plant *Impatiens sakeriana* (Fig. 1A) growing in mountain forests of Mount Cameroon. The flowers of *I. sakeriana* are visited by two sunbirds, *Cyanomitra oritis* (Cameroon sunbird) and *Cinnyris reichenowi* (northern double-collared sunbird), but not by insects (Janeček *et al.*, 2012; Chmel *et al.*, 2021; Sejfová *et al.*, 2021). *Cyanomitra oritis* is a very effective pollinator, whereas *Cinnyris reichenowi* is not and often steals nectar by piercing the corolla tube (Janeček *et al.*, 2011, 2015). The preferences of these two sunbirds were tested in an experimental cage where we placed, in addition to *I. sakeriana*, three other plant species that do not have bird pollination syndromes and are visited by other pollinators in addition to sunbirds in natural conditions (Chmel *et al.*, 2021). The experiment was performed at two sites, one in the mountain forest and one in the mid-elevation forest. Given that we used two plants growing in mountain habitats and two plants growing in mid-elevation forest habitats each time in the experimental cage, two local plants and two imported plants were used. The mountain species were *I. sakeriana* (Fig. 1A) and *Nuxia congesta* (Fig. 1B), and the mid-elevation forest species were *Tabernaemontana ventricosa* (Fig. 1C) and *Kigelia africana* (Fig. 1D). Additionally, to test whether the sunbird species feed in a different way on the target plant species in nature, we observed their natural feeding behaviours.

The following hypotheses and expectations were tested. First, niche partitioning occurs (i.e. where we

Figure 1. The studied plant and sunbird species. A, *Cyanomitra oritis* feeding on *Impatiens sakeriana*. B, male *Cinnyris reichenowi* on *Nuxia congesta*. C, *Cyanomitra oritis* feeding on *Tabernaemontana ventricosa*. D, *Kigelia africana*.

assumed that the two sunbird species occupy different food niches in natural conditions and differ in the ratios at which they visit the studied plant species). Second, the sunbird species differ in their preferences in experimental conditions, and these differences reflect the differences in natural feeding behaviours. We assume that in both systems, similar mechanisms (e.g. morphological matching) determine sunbird behaviour. Third, more familiar plants growing in the forest type where the experiment is conducted will be preferred over imported plants by local individuals of sunbirds. This expectation is based on the strong ability of nectarivorous birds to remember plants from which they drink (Healy & Hurly, 2003). Fourth, there is a general preference for ornithophilous plants; consequently, the ornithophilous plant *I. sakeriana* will be preferred by sunbirds over the less specialized *N. congesta* in the mid-elevation forest, where both are non-familiar to the sunbirds.

MATERIAL AND METHODS

STUDY SITES AND SPECIES

This study was carried out at two sites on the south-western slope of Mount Cameroon, the highest mountain in West Africa. One site was in the mountain forest near Mann's Spring (2200 m a.s.l), and the second was in the mid-elevation forest near the Crater Lake camp (1500 m a.s.l.). The sites were ~5 km from each other as the crow flies.

Cyanomitra oritis is a medium-sized, long-billed sunbird. On Mount Cameroon, individuals of this species weigh 10–14 g and have a bill length of 2.5–2.9 cm (Sejfová *et al.*, 2021). The elevational range of *Cyanomitra oritis* along the south-western slopes during the dry season is ~1100–2300 m a.s.l. *Cinnyris reichenowi* is a smaller sunbird with a short bill. On Mount Cameroon, individuals of this sunbird weigh 7–10 g and have a bill length of 1.6–2.2 cm

(Sejfová *et al.*, 2021). *Cinnyris reichenowi* has a more expansive range, occurring from ~1500 to 3700 m a.s.l.

The ornithophilous plant *I. sakeriana* (Fig. 1A; Balsaminaceae) has red, non-fragrant flowers with a nectar spur ~1.8 mm in length. The flowers are not reflective in the ultraviolet range (unpublished data, SJ). *Nuxia congesta* (Fig. 1B; Stilbaceae) is a mountain forest tree, with creamy white flowers with occasional mauve or purple, especially on the buds. The flowers have no clear pollination syndrome and possess ~5-mm-long floral tubes that are sweetly scented. According to our observations, they are most frequently visited by eusocial bees and moths. *Tabernaemontana ventricosa* (Fig. 1C; Apocynaceae) is a small tree or shrub with a moth pollination syndrome and is visited mainly by moths and butterflies. It has flowers ~3.5 cm in diameter with ~6-mm-long tubes. The flowers are white and sweetly scented. *Kigelia africana* (Fig. 1D; Bignoniaceae) is a tree with large red flowers that might have a bat or bat–bird mixed pollination syndrome (Chmel *et al.*, 2021; Newman *et al.*, 2021) and is visited by a wide spectrum of pollinators, including bats, birds, bees and bush babies (Baker, 1961; Ayensu, 1974; Namah *et al.*, 2019; Newman *et al.*, 2021). The funnel-shaped flowers are terminated by a floral tube ~24 mm in length. More information on the tube lengths and nectar traits of the target plants is provided in the Supporting Information (Table S1; for more details, see also Chmel *et al.*, 2021; Janeček *et al.*, 2021; Klomberg *et al.*, 2022).

OBSERVATIONS IN NATURAL CONDITIONS

For the purpose of this study, observational data for four target plant species were extracted from a large dataset that we collected to reconstruct complex flower–sunbird visitation networks (Chmel *et al.*, 2021; unpublished data, SJ). The herb *I. sakeriana* was monitored using security cameras (Vivotek IB8367RT), whereas the trees *N. congesta*, *T. ventricosa* and *K. africana*, which do not fit in the camera's field of view, were observed directly. In total, ten plants of *I. sakeriana* (219 h in total) were observed, with eight plants for each of the other three tree species (each 64 h in total). Note that in each forest type, only two plants were observed that grow there naturally (i.e. in the mountain forest, we observed *I. sakeriana* and *N. congesta*, and in the mid-elevation forest, we observed *T. ventricosa* and *K. africana*). Visitation frequencies (expressed as the number of visits per hour and hectare) were calculated using the frequencies on observed individual plants (visits per hour) and the abundance of flowering plant individuals counted along six 200 m × 10 m transects at each elevation where the experiment was performed.

OBSERVATIONS IN EXPERIMENTAL CONDITIONS

The experimental trials were performed in a cage measuring 1 m × 1 m × 1.7 m. In the cage, four perches were installed 125 cm above the ground, with a cross design. At the end of each 27-cm-long perch, the plants were placed in plastic flasks filled with water (Supporting Information, Fig. S1). The size of each plant reflected one naturally occurring attraction unit in the phenological stage at the time of the experiment. For *K. africana* and *I. sakeriana*, there was one flower (both species produce inflorescences, but at the time of the experiment, one opened flower per inflorescence was the most common); for *T. ventricosa*, there was an inflorescence with four or five opened flowers; and for *N. congesta*, there was one inflorescence (~300 tiny flowers). Both imported and local flowers were provided to the birds in each experimental trial. The birds for the experiment were collected by mist net in the forest where the experiment was performed. To prevent the use of one sunbird individual in several experimental trials, we marked the birds with metal rings after capture. For each trial, one sunbird individual was left in the cage for 45 min, and its behaviour was monitored using a GoPro camera. The camera observations were occasionally shorter owing to technical problems with the camera or longer for logistical reasons (e.g. checking mist nets). Nevertheless, we included all trials where the bird visited at least one plant, because these deviations were not systematic and had no (in the case of the first visit) or negligible (in the case of other preference parameters) impacts on preference estimates. For each of these trials, the positions of flowers were randomized. When needed, the flowers were replaced by fresh flowers. After the trial, the birds were released into the natural environment. In total, the experiment was performed with 78 sunbirds in the mountain forest (42 of *Cinnyris reichenowi* and 36 of *Cyanomitra oritis*) and with 64 birds in the mid-elevation forest (36 of *Cinnyris reichenowi* and 28 of *Cyanomitra oritis*). Each day, we performed 6–12 experimental trials from 07:30 to 18:00 h.

EVALUATION OF PREFERENCE AND STATISTICAL ANALYSES

Two-by-two bird × plant contingency tables containing count data on observed visits in natural conditions were tested using Fisher's exact test in R (R Core Team, 2020).

Three approaches were used to analyse the data and determine preferences from the cage experiments. First, only the first choices were considered. In this case, in the plant species × individual trial matrix, we allocated a value of one for the first visited species and zero for others. Second, all visited plants were treated equally, and all visited plant species were allocated a value of one, whereas all non-visited plants had a value of zero. Third, the visitation order was weighted. In this case, the first visited plants had a value of four in the matrix, the second visited plants had three, the third visited plants two, the fourth visited plants one, and the non-visited plants had zero. We used permutational analysis of variance (PERMANOVA) with a resemblance matrix based on Euclidean distances and the type III sum of squares to analyse the experimental preferences. PERMANOVA is non-parametric and tests the null hypothesis that the centroids and dispersion of the groups, defined by the measure of space, are equivalent among all groups. Moreover, inferences remain distribution free in such a test. We ran the analysis in the PERMANOVA program included in the software PRIMER (Anderson *et al.*, 2008). Differences between sexes were not tested because of the difficulty of recognizing the sexes in *Cyanomitra oritis*.

RESULTS

FORAGING BEHAVIOUR IN NATURAL CONDITIONS

According to the total number of sunbird visits in the mountain forest, there was a significant association between bird and plant species identity, indicating differences in feeding behaviour (Table 1; Fisher's exact test, $P < 0.001$). Although both species were observed more often on *N. congesta*, *Cyanomitra oritis* was more dominant than *Cinnyris reichenowi* on *I. sakeriana*.

Similar to the mountain forest, interactions in the mid-elevation forest around Crater Lake showed a significant association between sunbird and plant species identity when considering the numbers of visits arranged in a 2 × 2 matrix (i.e. two bird × two plant species; Fisher's exact test, $P < 0.0001$). *Cyanomitra oritis* was more dominant than *Cinnyris reichenowi* on *K. africana* and less dominant on *T. ventricosa*.

SUNBIRD PREFERENCES IN THE CAGE EXPERIMENT

We found significant effects of sunbird species identity and experimental location on feeding behaviour in the cage experiment (Table 2). The proportions of visits for individual plant species were similar irrespective of the method of preference evaluation used, except for a non-significant effect of bird identity when only the first visits were considered (Table 2; Fig. 2). There were three very clear patterns when considering individual plant species. First, *T. ventricosa* was the most preferred plant species. Second, *K. africana* was more preferred by *Cyanomitra oritis* than by *Cinnyris reichenowi*. Third, both sunbird species preferred *I. sakeriana* in the mountain forest, where it occurs naturally, compared with individuals in the mid-elevation forest, where it was imported for the experiment. When visits were combined for plants naturally growing in the mountain forest (*I. sakeriana* and *N. congesta*) and naturally growing in the mid-elevation forest (*T. ventricosa* and *K. africana*), only locality had a significant effect when considering preferences as weighted visits (Table 2), with a higher tendency to visit local species (Fig. 2C).

DISCUSSION

Our field observations confirmed the niche partitioning hypothesis. In natural conditions, individual sunbird species differed in the ratios of visits to both mountain and mid-elevation plant species pairs. As expected, the short-billed sunbird, *Cinnyris reichenowi*, had higher short-tube plant/long-tube plant visitation ratios (i.e. *N. congesta*/*I. sakeriana* and *T. ventricosa*/*K. africana* ratios) than the long-billed sunbird, *Cyanomitra oritis*. These results support the idea that plant and bird traits are important for structuring bird–plant assemblages (Geerts & Pauw, 2009; Janeček *et al.*, 2012; Maglianesi *et al.*, 2014; Sonne *et al.*, 2019). However, we would like to point out that these differences in feeding observed in nature are relative (i.e. when sunbird species are compared with each other). We did not consider plant abundances; consequently, we did not evaluate, during

Table 1. Number of total visits observed (total) and number of visits expressed as visitation frequency per hectare [visits per hectare per hour (VHH)] by *Cyanomitra oritis* and *Cinnyris reichenowi* to different plant species in natural conditions

Plant species	*Cyanomitra oritis*		*Cinnyris reichenowi*		Forest type
	Total	VHH	Total	VHH	
Nuxia congesta	40	1.56	1619	63.19	Mountain forest
Impatiens sakeriana	31	0.24	20	0.15	Mountain forest
Tabernaemontana ventricosa	11	16.33	167	247.89	Mid-elevation forest
Kigelia africana	125	35.81	66	18.91	Mid-elevation forest

Table 2. Effects of sunbird species and location of experiment on sunbird preferences

	d.f.	(a) First visits		(b) All unweighted visits		(c) Weighted visits	
		F_{ps}	*P*-value	F_{ps}	*P*-value	F_{ps}	*P*-value
Preferences for individual plants							
Lc	1	4.47	**0.007**	3.44	**0.017**	7.36	**0**
Bs	1	1.62	0.181	3.41	**0.017**	5.73	**0.001**
Lc × Bs	1	0.9	0.423	0.53	0.675	0.34	0.765
Preferences for mountain vs. mid-elevation forest plants							
Lc	1	3.04	0.082	2.46	0.082	8.29	**0.001**
Bs	1	0.01	0.925	0.74	0.5	0.67	0.493
Lc × Bs	1	0.64	0.436	0.25	0.804	0.37	0.677

Preference estimates were calculated by PERMANOVA using three approaches: (1) first visits; (2) all unweighted visits; and (3) weighted visits (for details, see Material and Methods section). Individual plant preferences reflect preferences for individual plant species; preferences for mountain vs. mid-elevation forest plants consider the visits to the mountain (*Impatiens sakeriana* + *Nuxia congesta*) and mid-elevation (*Kigelia africana* + *Tabernaemontana ventricosa*) plants combined. Significant p-values ($p<0.05$) are in bold.
Abbreviations: Bs, bird species; Lc, locality; Lc × Bs, interaction between the factors locality and bird species; F_{ps}, pseudo F-ratio.

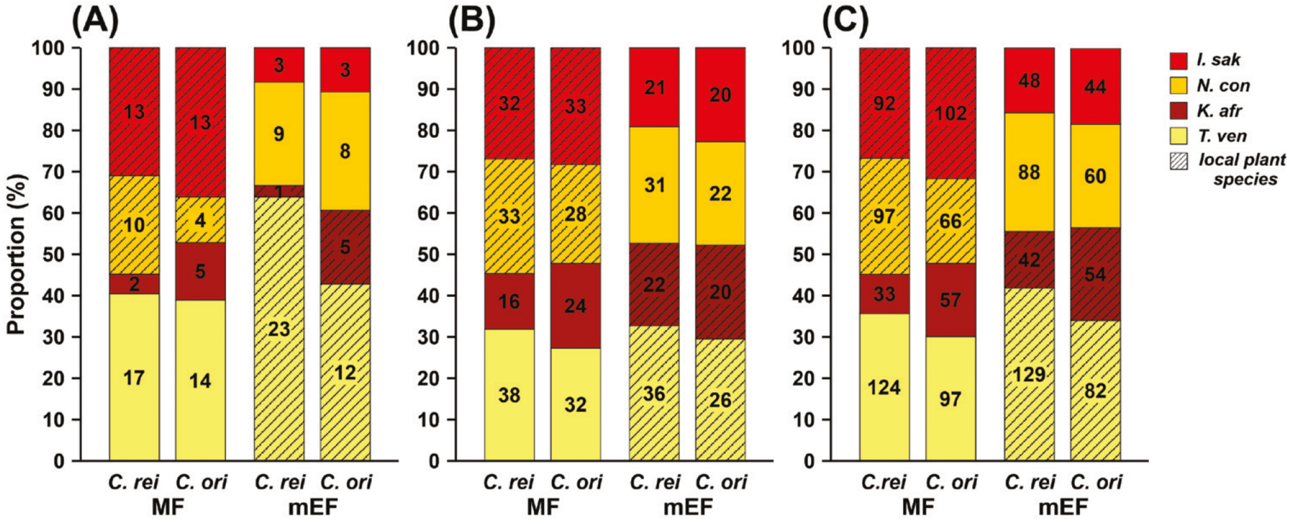

Figure 2. A, proportions of plant preferences in the case of first choices of sunbirds in the trials. The data presented are the numbers of trials when the plants were the first to be visited. B, proportions of plant preferences in the case where all visited plant species were considered without regard to visit order. The data presented are the numbers of trials when plants were visited in any order. C, proportions of plant preferences in the case where plant species visits were weighted according to visit order, as follows: first visited plant species, four points; second visited plant species, three points; third visited plant species, two points; fourth visited plant species, one point; and non-visited plant species, zero points. The sum of the points for individual plants is reported. Abbreviations: mEF, mid-elevation forest; MF, mountain forest.

the field observations, preferences for one plant species over the other plant species. In other words, the conclusion that *Cinnyris reichenowi* had a higher *N. congesta*/*I. sakeriana* visitation ratio does not mean that *Cinnyris reichenowi* prefers *N. congesta* to *I. sakeriana*.

The preferences of the birds observed in experimental conditions reflected, to a large extent, the feeding pattern in natural conditions. *Cyanomitra oritis* was more often observed on *K. africana* than was *Cinnyris reichenowi* in both natural and experimental conditions. Likewise, as in the case of feeding behaviour, the *N. congesta*/*I. sakeriana* visitation ratio was higher for *Cinnyris reichenowi* in the mountain forest cage experiment. Nevertheless, the *N. congesta*/*I. sakeriana* visitation ratios of both sunbird species in the cage were much more similar. The cage experiment thus indicates that the feeding behaviour observed in nature might be driven largely by factors other than sunbird preferences. We assume that interspecific differences in the abilities of birds to find and exploit individual plant species effectively, together with interspecific competition, might be of great importance. These suggestions concur with the findings of other studies that *Cyanomitra oritis* has a faster drinking speed (amount of time taken to consume nectar; Janečková *et al.*, 2020) and can handle the flowers of *I. sakeriana* more quickly than *Cinnyris reichenowi* (Sejfová *et al.*, 2021). The stronger relationship between *Cyanomitra oritis* and *I. sakeriana* was also indicated by the higher pollination effectiveness of the former (Janeček *et al.*, 2011) and its strictly legitimate visits to the flowers (Janeček *et al.*, 2011, 2015).

In the cage experiment, the sunbirds occasionally visited all plant species, irrespective of pollination syndromes and whether they were local or imported. Moreover, the most preferred plant was *T. ventricosa*, which has a moth pollination syndrome. These observations concur with those of other studies showing exploratory behaviour in hummingbirds, which enables them to discover and use new resources (e.g. Collias & Collias, 1968). The preference for local plants was rather weak and was significant only when considering weighted visits. Nevertheless, this effect was evident for the only plant with the bird pollination syndrome, *I. sakeriana*. The higher proportion of visits to *I. sakeriana* by sunbirds that were mist-netted in the mountain forest (i.e. the same habitat where *I. sakeriana* grows) indicates the importance of associative learning of the plant species bearing bird pollination syndromes with rewards. In other words, the sunbirds in the mountain forest associated the appearance of *I. sakeriana* flowers with a rich nectar reward (for information on nectar production by *I. sakeriana*, see Bartoš *et al.*, 2012). Nevertheless, *I. sakeriana* was not preferred over *N. congesta* when both were presented to the mid-elevation forest sunbirds. This finding is interesting given that, according to previous studies, mid-elevation forest sunbirds also visit flowers with bird pollination syndromes (Bartoš & Janeček, 2014; Janeček *et al.*, 2015). Consequently, the extremely low proportion of visits for *I. sakeriana* in the mid-elevation forest questions the hypothesis that not only plants with specific bird pollination syndromes but also those with general bird pollination syndromes can be learned by birds and that the birds can easily recognize even unfamiliar plants with such a syndrome (Grant, 1966; Schiestl & Johnson, 2013).

Although our study did not target individual floral traits, our results support trait-related discussions. If we consider the previous studies demonstrating that *I. sakeriana* is not visited by insects (Janeček *et al.*, 2011; Chmel *et al.*, 2021) and the results of the present study showing that sunbirds have much lower preferences for *I. sakeriana* when they do not share the same habitat, we must agree with the idea that red colours are likely to have evolved to filter out bees from the bird pollination systems rather than to attract birds (Lunau *et al.*, 2011; Bergamo *et al.*, 2016; de Camargo *et al.*, 2019; Coimbra *et al.*, 2020).

More generally speaking, the results showing that birds do not care much if the plant bears a bird pollination syndrome (see also Chmel *et al.*, 2021) challenge the idea that signalling traits of ornithophilous flowers evolved to attract bird pollinators. Rather, it seems that from the point of view of the birds, there is no reason for bird pollination syndrome plants to look the way they do. In other words, there is no reason for birds to not select, for example, white, fragrant flowers if they offer enough nectar. This idea is also supported by studies showing a much greater importance of nectar production than of flower signalling traits for bird visitation (Schmid *et al.*, 2016; Chmel *et al.*, 2021). Moreover, in addition to colour, the signalling function of flower shape and floral scent in bird pollination syndromes, such as the dominant role of pollinator-mediated selection in their evolution, is controversial. The tubular shape is rather useful for hiding nectar and filtering out visitors with short mouthparts, and the absence of scent in some ornithophilous species (Knudsen *et al.*, 2004) might be an adaptation for insect avoidance rather than for bird attraction. We suggest that ornithophilous flowers should be considered a 'private' part of the much broader bird feeding niche (i.e. a part that is not readily available to other animals). This status provides high specialization to birds, which secures high pollination effectiveness for the plant but does not represent an adaptation increasing sensory attractiveness to bird visitors.

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DATA AVAILABILITY

The data underlying this article will be shared on reasonable request to the corresponding author.

REFERENCES

Abrahamczyk S, **Poretschkin C**, **Renner SS. 2017.** Evolutionary flexibility in five hummingbird/plant mutualistic systems: testing temporal and geographic matching. *Journal of Biogeography* **44:** 1847–1855.

Anderson MJ, **Gorley RN**, **Clarke KR. 2008.** *PERMANOVA+ for PRIMER: guide to software and statistical methods*. Plymouth: PRIMER-E.

Araujo AC, **Sazima M. 2003.** The assemblage of flowers visited by hummingbirds in the "capões" of Southern Pantanal, Mato Grosso do Sul, Brasil. *Flora - Morphology, Distribution, Functional Ecology of Plants* **198:** 427–435.

Ayensu ES. 1974. Plant and bat interactions in West Africa. *Annals of the Missouri Botanical Garden* **61:** 702–727.

Baker HG. 1961. The adaptation of flowering plants to nocturnal and crepuscular pollinators. *The Quarterly Review of Biology* **36:** 64–73.

Bartoš M, **Janeček Š. 2014.** Polinator-induced twisting of flowers sidesteps floral architecture constraints. *Current Biology* **24:** R793–R795.

Bartoš M, **Janeček Š**, **Padyšáková E**, **Patáčová E**, **Altman J**, **Pešata M**, **Kantorová J**, **Tropek R. 2012.** Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: a comparison with six other co-flowering species. *South African Journal of Botany* **78:** 63–74.

Bené F. 1941. Experiments on the color preference of black-chinned hummingbirds. *The Condor* **43:** 237–242.

Bergamo PJ, **Rech AR**, **Brito VL**, **Sazima M. 2016.** Flower colour and visitation rates of *Costus arabicus* support the 'bee avoidance' hypothesis for red-reflecting hummingbird-pollinated flowers. *Functional Ecology* **30:** 710–720.

Bergamo PJ, **Wolowski M**, **Maruyama PK**, **Vizentin-Bugoni J**, **Carvalheiro LG**, **Sazima M. 2017.** The potential indirect effects among plants via shared hummingbird pollinators are structured by phenotypic similarity. *Ecology* **98:** 1849–1858.

Chmel K, **Ewome FL**, **Gómez GU**, **Klomberg Y**, **Mertens JEJ**, **Tropek R**, **Janeček S. 2021.** Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective. *Oikos* **130:** 1411–1424.

Coimbra G, **Araujo C**, **Bergamo PJ**, **Freitas L**, **Rodríguez-Gironés MA. 2020.** Flower conspicuousness to bees across pollination systems: a generalized test of the bee-avoidance hypothesis. *Frontiers in Plant Science* **11:** 558684.

Collias NE, **Collias EC. 1968.** Anna's hummingbirds trained to select different colors in feeding. *The Condor* **70:** 273–274.

Cronk Q, **Ojeda I. 2008.** Bird-pollinated flowers in an evolutionary and molecular context. *Journal of Experimental Botany* **59:** 715–727.

Darwin C. 1862. *On the various contrivances by which British and foreign orchids are fertilized*. London: John Murray.

de Camargo MGG, **Lunau K**, **Batalha MA**, **Brings S**, **Brito VLG**, **Morellato LPC. 2019.** How flower colour signals allure bees and hummingbirds: a community-level test of the bee avoidance hypothesis. *New Phytologist* **222:** 1112–1122.

Ehrlén J. 2015. Selection on flowering time in a life-cycle context. *Oikos* **124:** 92–101.

Faegri K, **van der Pijl L. 1979.** *The principles of pollination ecology*. Pergamon Press, Oxford, England.

Fenster CB, **Armbruster S**, **Wilson P**, **Dudash MR**, **Thomson JD. 2004.** Pollination syndromes and floral specialization. *Annual Review of Ecology and Systematics* **35:** 375–403.

Fenster CB, **Reynolds RJ**, **Williams CW**, **Makowsky R**, **Dudash MR. 2015.** Quantifying hummingbird preference for floral trait combinations: the role of selection on trait interactions in the evolution of pollination syndromes. *Evolution* **69:** 1113–1127.

Geerts S, **Pauw A. 2009.** Hyper-specialization for long-billed bird pollination in a guild of South African plants: the malachite sunbird pollination syndrome. *South African Journal of Botany* **75:** 699–706.

Goldsmith KM, **Goldsmith TH. 1982.** Sense of smell in the Black-chinned Hummingbird. *The Condor* **84:** 237–238.

Goldsmith TH, **Goldsmith KM. 1979.** Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri*. *Journal of Comparative Physiology* **130:** 209–220.

Grant KA. 1966. A hypothesis concerning the prevalence of red coloration in California hummingbird flowers. *The American Naturalist* **100:** 85–97.

Hart NS, **Hunt DM. 2007.** Avian visual pigments: characteristics, spectral tuning, and evolution. *The American Naturalist* **169:** S7–S26.

Healy SD, **Hurly TA. 2003.** Cognitive ecology: foraging in hummingbirds as a model system. *Advances in Study of Behavior* **32:** 325–359.

Janeček Š, **Bartoš M**, **Njambo KY. 2015.** Convergent evolution of sunbird pollination systems of *Impatiens* species in tropical Africa and hummingbird systems of the New World. *Biological Journal of the Linnean Society* **115:** 127–133.

Janeček Š, **Chmel K**, **Ewome FL**, **Hrubá K**, **Klomberg Y**, **Kobe IN**, **Kouede RD**, **Mertens JEJ**, **Njie MM**, **Tropek R. 2021.** Differences in nectar traits between ornithophilous and entomophilous plants on Mount Cameroon. *Plants* **10:** 1161.

Janeček Š, **Chmel K**, **Gómez GU**, **Janečková P**, **Chmelová E**, **Sejfová Z**, **Ewome FL. 2020.** Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution* **10:** 1784–1793.

Janeček Š, **Patáčová E**, **Bartoš M**, **Padyšáková E**, **Spitzer L**, **Tropek R. 2011.** Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? *Oikos* **120:** 178–183.

Janeček Š, **Riegert J**, **Bartoš M**, **Hořák D**, **Reif J**, **Padyšáková E**, **Fainová D**, **Antczak M**, **Pešata M**, **Mikeš V**, **Patáčová E**, **Altman J**, **Kantorová J**, **Hrázský Z**, **Brom J**, **Doležal J. 2012.** Food selection by avian floral visitors: an important aspect of plant–flower interactions in West Africa. *Biological Journal of the Linnean Society* **107:** 355–367.

Janečková P, Sejfová Z, Janeček Š, Chmel K, Chmelová E, Ewome FL. 2020. Behavioural correlates of drinking speed in two West African sunbird species. *Bird Study* **67:** 540–542.

Klomberg Y, Tropek R, Mertens JEJ, Kobe IN, Hodeček J, Raška J, Fominka NT, Souto-Vilarós D, Janečková P, Janeček Š. 2022. Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. *Ecology Letters* **25:** 839–850.

Knudsen JT, Tollstein L, Groth I, Bergström G, Raguso RA. 2004. Trends in floral scent chemistry in pollination syndromes: floral scent composition in hummingbird-pollinated taxa. *Biological Journal of the Linnean Society* **146:** 191–199.

Lunau K, Papiorek S, Eltz T, Sazima M. 2011. Avoidance of achromatic colours by bees provides a private niche for hummingbirds. *The Journal of Experimental Biology* **214:** 1607–1612.

Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M. 2014. Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics. *Ecology* **95:** 3325–3334.

Maruyama PK, Oliveira GM, Ferreira C, Dalsgaard B, Oliveira PE. 2013. Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. *Naturwissenschaften* **100:** 1061–1068.

Mayfield MM, Waser NM, Price MV. 2001. Exploring the 'most effective pollinator principle' with complex flowers: bumblebees and *Ipomopsis aggregata*. *Annals of Botany* **88:** 591–596.

Miller RS, Miller RE. 1971. Feeding activity and color preference of ruby-throated hummingbirds. *The Condor* **73:** 309–313.

Namah J, Midgley JJ, Kruger LM. 2019. Reproductive biology of the sausage tree (*Kigelia africana*) in Kruger National Park, South Africa. *Koedoe* **61:** a1512.

Newman E, Govender K, van Niekerk S, Johnson SD. 2021. The functional ecology of bat pollination in the African sausage tree *Kigelia africana* (Bignoniaceae). *Biotropica* **53:** 477–486.

Nsor CA, Godsoe W, Chapman HM. 2019. Promiscuous pollinators—Evidence from an Afromontane sunbird–plant pollen transport network. *Biotropica* **51:** 538–548.

Ollerton J, Alarcon R, Waser NM, Price MV, Watts S, Cranmer L, Hingston A, Peter CI, Rotenberry J. 2009. A global test of the pollination syndrome hypothesis. *Annals of Botany* **103:** 1471–1480.

Padyšáková E, Bartoš M, Tropek R, Janeček Š. 2013. Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae). *PLoS One* **8:** e59299.

Pleasants JM, Waser NM. 1985. Bumblebee foraging at a 'hummingbird' flower: reward economics and floral choice. *American Midland Naturalist* **114:** 283–291.

Ramírez SR, Eltz T, Fujiwara MK, Gerlach G, Goldman-Huertas B, Tsutsui ND, Pierce NE. 2011. Asynchronous diversification in a specialized plant-pollinator mutualism. *Science* **333:** 1742–1746.

R Core Team. 2020. *R: a language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.

Rothshild LW. 1903. *A revision of the lepidopterous family Sphingidae*. Aylesbury: Hazell, Watson & Viney.

Schiestl FP, Johnson SD. 2013. Pollinator-mediated evolution of floral signals. *Trends in Ecology & Evolution* **28:** 307–215.

Schmid B, Nottebrock H, Esler KJ, Pagel J, Pauw A, Böhning-Gaese K, Schurr FM, Schleuning M. 2016. Responses of nectar-feeding birds to floral resources at multiple spatial scales. *Ecography* **39:** 619–629.

Schmid S, Schmid VS, Zillikens A, Steiner J. 2011. Diversity of flower visitors and their role for pollination in the ornithophilous bromeliad *Vriesea friburgensis* in two different habitats in Southern Brazil. *Ecotropica* **17:** 91–102.

Sejfová Z, Mlíkovský J, Ewome FL, Janečková P, Klomberg Y, Njie MM, Janeček Š. 2021. Sunbirds' tendency to hover: the roles of energetic rewards, inflorescence architecture and rain. *Journal of Avian Biology* **52:** e02818.

Sherman AR. 1913. Experiments in feeding hummingbirds during seven summers. *The Wilson Bulletin* **25:** 153–166.

Snow BK, Snow DW. 1972. Feeding niches of hummingbirds in Trinidad valley. *Journal of Animal Ecology* **41:** 471–485.

Sonne J, Zanata TB, Martín-González AM, Cumbicus Torres NL, Fjeldså J, Colwell RK, Tinoco BA, Rahbek C, Dalsgaard B. 2019. The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. *Biotropica* **51:** 205–218.

Stiles FG. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. *Annals of the Missouri Botanic Garden* **68:** 323–351.

Vázquez DP, Aizen MA. 2004. Asymmetric specialization: a pervasive feature of plant–pollinator interactions. *Ecology* **85:** 1251–1257.

Vizentin-Bugoni J, Maruyama PK, Sazima M. 2014. Processes entangling interactions in communities: forbidden links are more important than abundance in a hummingbird–plant network. *Proceedings of the Royal Society B: Biological Sciences* **281:** 20132397.

Wang Q, Li Y, Pu X, Zhu L, Tang Z, Liu Q. 2013. Pollinators and nectar robbers cause directional selection for large spur circle in *Impatiens oxyanthera* (Balsaminaceae). *Plant Systematics and Evolution* **299:** 1263–1274.

Waser NM. 2006. Specialization and generalization in plant–pollinator interactions: a historical perspective. In: Waser NM, Ollerton J eds. *Plant–pollinator interactions, from specialization to generalization*. Chicago: The University Chicago Press, 3–17.

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J. 1998. Generalization in pollination systems, and why it matters. *Ecology* **77:** 1043–1060.

Wester P. 2014. Feeding on the wing: hovering in nectar-drinking Old World birds – more common than expected. *Emu* **114:** 171–183.

Westerkamp C. 1990. Bird-flowers: hovering versus perching exploitation. *Botanica Acta* **103:** 366–371.

Whittall JB, **Hodges SA. 2007.** Pollinator shifts drive increasingly long nectar spurs in columbine flowers. *Nature* **447:** 706–709.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Spur lengths and nectar traits of the target plant species.
Figure S1. Experimental cage. A, exterior view. B, interior view.

SUPPORTING INFORMATION CHAPTER III

Mundi, O., Awa II, T., Chmel, K., Ewome, F.L., **Uceda-Gómez, G.**, Janečková, P., & Janeček, Š. (2022). The ornithophily of *Impatiens sakeriana* does not guarantee a preference by sunbirds. *Biological Journal of the Linnean Society*, 137, 240-249. https://doi.org/10.1093/biolinnean/blac083

Table S1. Spur lengths and nectar traits of the target plant species. Tube length was measured by digital callipers. To measure nectar production over 24 hrs, the flowers were covered by a dense net to avoid nectar consumption by visitors. After this period, the nectar volume was measured using 5 µl microcapillary tubes, and the concentration was determined by a Pal-1 (Atago Co.) pocket refractometer (for more details, see Janeček *et al.*, 2021a; Chmel *et al.*, 2021; Klomberg *et al.*, 2022 cited in the main text). * We measured the narrow tube of the calyx and not the whole flower, including the wide part where a sunbird can insert its head.

	Tube length (cm)			**24 hrs nectar production (µl flower $^{-1}$)**			**Nectar sugar concentration (% w/w)**		
	mean	***SD***	***n***	***mean***	***SD***	***n***	***mean***	***SD***	***n***
Impatiens sakeriana	1.8	0.19	7	14.7	11	15	22.4	5.4	15
Nuxia congesta	0.46	0.07	7	0.84	0.72	18	27.7	10.16	18
Tabernaemontana ventricosa	0.61	0.02	6	4.66	3.09	30	20.2	8.14	29
Kigelia africana	2.4*	0.33	5	49	105.3	24	16.6	5.24	24

Figure S1: Experimental cage; A/ exterior view; B/ interior view

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Research

Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective

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Many tropical plants are pollinated by birds and several bird phylogenetical lineages have specialised to a nectar diet. The long-assumed, intimate ecological and evolutionary relationship between ornithophilous plants and phenotypically specialised nectarivorous birds has nevertheless been questioned in recent decades, where such plant–pollinator interactions have been shown to be highly generalised.

In our study, we analysed two extensive interaction datasets: bird–flower and insect–flower interactions, both collected on Mt Cameroon, west-central Africa. We tested if: 1) insects and birds interact with distinct groups of plants; 2) plants with a typical set of ornithophilous floral traits (i.e. bird pollination syndrome) interact mainly with birds; 3) birds favour plants with bird pollination syndrome and; 4) if and how the individual floral traits and plant level nectar production predict bird visitation.

Bird-visited plants were typically also visited by insects, while approximately half of the plants were visited by insects only. We confirmed the validity of the bird pollination syndrome hypothesis, as plants with bird-pollination syndrome traits were visited by birds at a higher rate and mostly hosted a lower frequency of visiting insects. However, these ornithophilous plants were not more attractive than the other plants for nectar-feeding birds. Nectar production per plant individual was a better predictor of bird visitation than any other floral trait traditionally related to the bird pollination syndrome. Our study thus demonstrated the highly asymmetrical relationship between ornithophilous plants and nectarivorous birds.

Keywords: floral choice, floral traits, Mount Cameroon National Park, nectar resource, nectarivorous birds, pollination

Introduction

Most tropical plants rely on animals for pollination (Ollerton et al. 2011) and floral food rewards are important parts of the diet for many animal groups. Consequently, in tropical rainforests approximately 98% of flowering plants are estimated to be

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animal-pollinated (Bawa 1990). Although most of them depend on insect pollinators (Proctor et al. 1996), vertebrates, particularly birds and bats, also represent important pollen vectors in tropical pollination networks (Fleming and Muchhala 2008, Zanata et al. 2017). While there are a number of nectar feeding bird species across different families (Proctor et al. 1996), we recognize three main families of flower specialists globally: hummingbirds (Trochilidae) in the Neotropics, sunbirds (Nectariniidae) in the Old World, and honey-eaters (Meliphagidae) in Australasia (Fleming and Muchhala 2008).

The concept of mutualistic evolutionary adaptations in plant–pollinator interactions was first put forth by Darwin's 'evolutionary race' (Darwin, 1862). This concept includes, among others, the step by step co-evolution where both partners (or partner groups) continuously increase the level of their co-adaptations, gradually producing a system characterised by high specialisation on both sides. Nevertheless, the adaptations of some plants can result from a one-sided evolutionary pressure to already pre-adapted pollinators (i.e. pollinator shift, Wasserthal 1997, Whittall and Hodges 2007). Such processes can also be the reason why radiations of some plant lineages have been much younger than radiations of their pollinators (Tripp and McDade 2013, Givnish et al. 2014).

Pollination syndromes are one of the central concepts of plant adaptation, where plants pollinated by the same pollinator group are hypothesised to share similar floral traits via convergent evolution (Faegri and van der Pijl 1979, Fenster et al. 2004, Rosas-Guerrero et al. 2014). Within the bird pollination syndrome, ornithophilous flowers tend to be red or orange, tubular with copious nectar, and lack characters associated with other syndromes, such as a strong scent or presence of nectar guides (Faegri and van der Pijl 1979, Fenster et al. 2004, Cronk and Ojeda 2008, Fenster et al. 2015). In parallel, Stiles (1981) defined the 'syndrome of anthophily' for specialised nectarivorous birds, which includes morphological, physiological, and behavioural adaptations of birds related to nectarivory.

In recent decades however, community-wide studies have demonstrated that ecological reality and co-evolution processes can be much more complicated, and that the close relationships in foraging/pollination systems are rather exceptional (Waser et al. 1996). For example, specialised nectarivorous birds are frequent visitors of non-ornithophilous plants (Araujo and Sazima 2003, Maruyama et al. 2013), where they may act as thieves (Rocca and Sazima 2006, Janeček et al. 2007, Padyšáková et al. 2013), although in other cases also as co-pollinators (Wolff et al. 2003, Freitas et al. 2006, Aguilar-Rodríguez et al. 2016). Conversely, although plants with the bird-pollination syndrome are often pollinated by birds (Johnson and Wester 2017), they may also host other visitors (e.g. bumblebees – Pleasants and Waser 1985, Urcelay et al. 2006, bees – Schmid et al. 2011, Wilson et al. 2004). Additionally, the applicability of the bird pollination syndrome differs regionally (Brown and Hopkins 1995, Fleming and Muchhala 2008) or along environmental gradients, such as elevation (Araujo and Sazima 2003, Krömer et al. 2006, Dalsgaard et al. 2011, Partida-Lara et al. 2018) or precipitation (Dalsgaard et al. 2011, Maruyama et al. 2013). Finally, we must acknowledge that a proportion of plants are adapted to a generalized pollination system, making phenotypic-based predictions of its primary pollinator impossible (Waser et al. 1996, Fenster et al. 2004, Ollerton et al. 2009, Dellinger 2020).

The pollination syndrome hypothesis, together with coevolutionary theory, suggests that the selection pressures imposed by pollinators are the most important drivers of floral evolution (Stebins 1970, Ashworth et al. 2015). Nevertheless, individual floral traits could evolve as a response to different selection agents, e.g. herbivores (Strauss et al. 2004) or abiotic conditions (Galen 2000). Considering the bird pollination syndrome, it has been shown for example that the most specialized nectarivorous birds, hummingbirds, have no preference for red colouration (Collias and Collias 1968, Miller and Miller 1971). Instead the red colour may sensorially exclude bees (a group with no photoreceptors for red light) from ornithophilous flowers (Bergamo et al. 2016, Coimbra 2020). Therefore, while the most efficient pollinators may truly coincide with the defined pollination syndrome (Rosas-Guerrero et al. 2014), from the pollinators' perspective, floral choice may likely be simplerdetermined only by the quantity and quality of food rewards (Waser 1983, Pleasants and Waser 1985, Stromberg and Johnsen 1990, Essenberg 2012, Schmid et al. 2016). Nevertheless, this resource-motivated selection has seen indirect support. Studies have suggested that a substantial proportion of flowers are pollinated by several different pollinators, and that pollinators visit flowers of multiple plant species often belonging to different pollination syndromes (Herrera 1996, Waser et al. 1996).

In this study, we test the validity of the bird pollination syndrome hypothesis and explore the flower-bird relationships on Mount Cameroon, West/Central Africa. Our analyses were performed in two complementary ways: First, we used a simple conceptual model to test: 1) if birds and insects prefer distinct groups of plants (Fig. 1A); 2) whether plants with the bird pollination syndrome were favoured by birds but avoided by insects (Fig. 1B) and; 3) if birds feed mainly on the ornithophilous plants (Fig. 1C). Second, we tested if 4) any floral traits related to the bird pollination syndrome predicted bird visitation and; 5) whether these traits were better predictors than the nectar production of the whole plant individual.

Methods

Study site

All datasets were collected in tropical rainforests on the south-western slope of Mt Cameroon (Cameroon), the highest mountain of West Africa. On this slope, primary forests

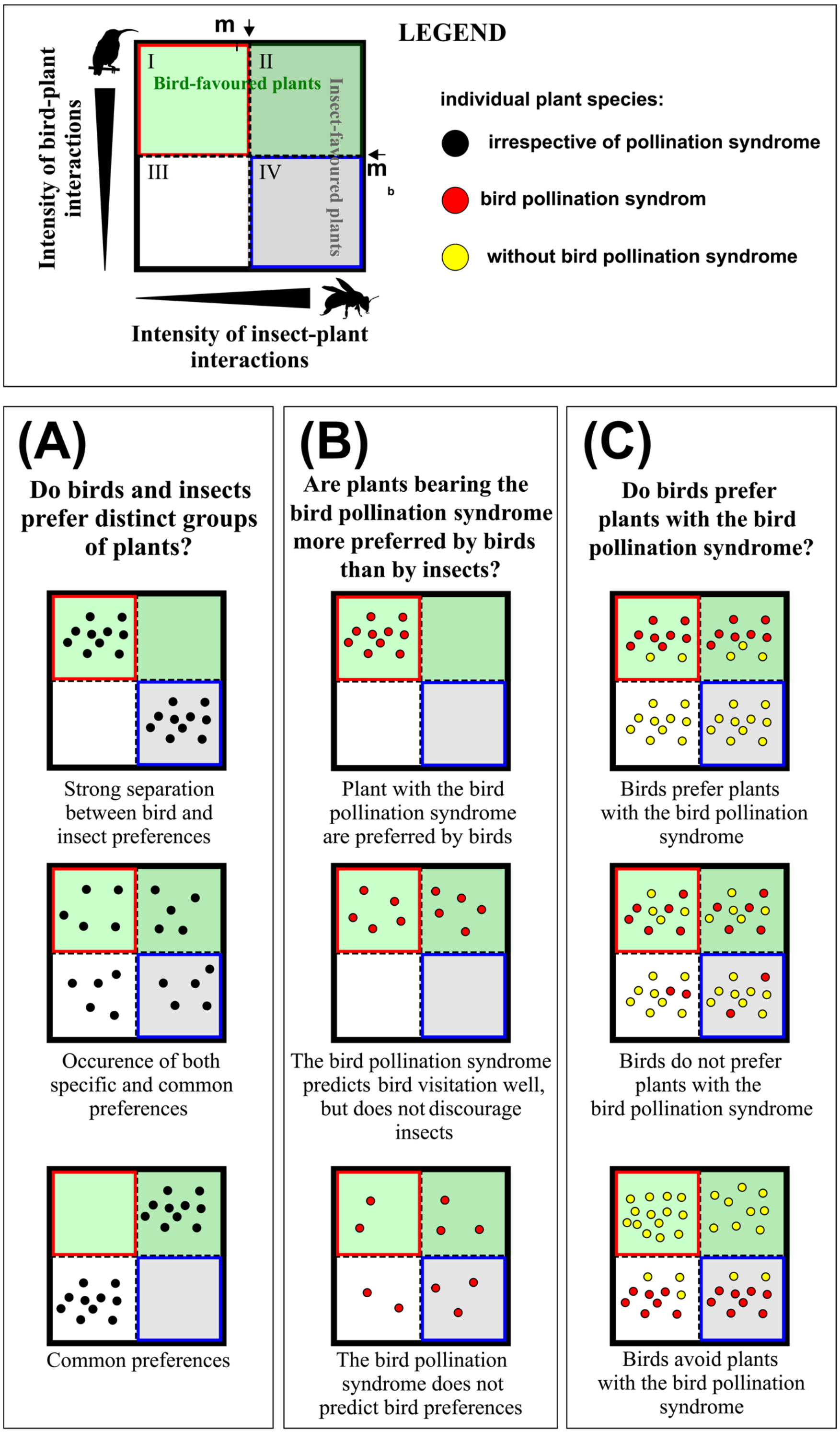


Figure 1. Conceptual model where plant species are organized in the space defined by the axes of bird–plant and insect–plant interactions intensity: I) a bird–plant interaction zone with a high intensity of bird–plant interactions (red border); II) a zone with a high intensity of both bird and insect interactions; III) a zone with low intensity interactions by both pollinator groups; and IV) an insect–plant interaction zone with a high intensity of insect–plant interactions (blue border). m_i – median of the intensity of insect–plant interactions dividing the space for the insect preferred (zones II and IV) and nonpreferred (zones I and III) plants; m_b – median of the intensity of bird–plant interactions dividing the space to bird preferred (zones I and II) and bird non-preferred (zones III and IV) plants. (A), (B) and (C) show possible scenarios related to our target questions.

are preserved from approximately 400 m a.s.l. up to the natural treeline at approximately 2200 m a.s.l. (Cable and Cheek 1998). The climate of Mount Cameroon comprises of a period of heavy rains, which occur between June and October, and a dry season which extends from November to May, with an annual rainfall usually exceeding 10 000 mm (Lefevre 1967, Maicher et al. 2020). The data were collected at four sites distributed along the elevational gradient of the mountain: 1) Drink Garri (650 m a.s.l.) – lowland tropical rainforest with abundant trees from the family Caesalpiniaceae; 2) PlanteCam (1100 m a.s.l.) – mid- elevation forest partly disturbed by elephants; 3) Crater Lake (1450 m a.s.l.) – submontane forest strongly disturbed by elephants; 4) Mann's Spring (2200 m a.s.l.) – mountain forest close to the treeline (Maicher et al. 2020). At each site, we collected data both in the wet and dry seasons. The sampling included vegetation surveys along six 200 × 10 m permanent transects per sites, along which we estimated the abundance of flowering plants, together with numbers of flowers per plant individual. Transects were situated at least 100 m apart so as to account for some environment heterogeneity at each locality.

Floral traits

Based on Faegri and van der Pijl (1979) and Ollerton et al. (2009), we selected six floral traits related to the bird pollination syndrome, including floral size (averaged in asymmetric flowers), tube length, odour (weak–no versus moderate–strong), colour (as sensed by humans), nectar guides (presence versus absence), and nectar sugar production (mg) per flower. Additionally, we calculated the resource quantity by multiplying the latter trait with the number of flowers per plant, i.e. average nectar production per individual of each species. All measured trait values of the studied plant species are listed in the Supporting information. The morphological floral trait measurements were done using a digital calliper. Ideally, a minimum of five replicates of each plant species were measured. If sufficient replicates were not found within the transects, we broadened the search area to the adjoining vegetation. We covered the flowers with mesh bags for a 24-h period before the nectar measurement allowing us to compare the nectar production of individual plant species. If nectar was abundant, it was extracted and its volume was measured using a Hamilton syringe or a capillary tube following Bartoš et al. (2012). The nectar concentration was then measured with the Pal-1 (Atago Co) pocket refractometer. Subsequently, the amount of sugar per flower was calculated based on the nectar volume and its concentration. Flowers which produced low volumes of nectar were washed with distilled water which was then collected in an eppendorf tube. Later in the field camp, we added ethanol to achieve 50% concentration and boiled the solution to avoid any possible enzymatic degradation during transport to the lab (Chlumská et al. 2014). In the lab, we dried the samples, transferred them into constant volume, and the sugar amounts were measured using an Ionic Chromatograph ICS-3000 with an electrochemical detector and CarboPac PA1 column. Due to their rarity or inaccessibility, we were not able to collect values of sugar production for all plant species that flowered at the study sites, these were therefore omitted from the dataset, with the exception of *Phragmanthera kamerunensis* As this species represents an important nectar resource for bird visitors (Janeček et al. unpubl.), we used the sugar content (average value in closed flowers) from Gill and Wolf (1975) who explored the energetics of a similar East African species *Phragmanthera dshallensis*.

Based on the traditional definitions of pollination syndromes (Faegri and van der Pijl 1979, Fenster et al. 2004, Cronk and Ojeda 2008), we considered flowers of plants to fit into the bird pollination syndrome if they met all these preconditions: 1) provided sufficient nectar reward (> 0.3 μl per flower); 2) did not produce a strong odour; 3) had a long wavelength, i.e. orange/red colour; 4) were of tubular shape (tubelength > 1 cm); 5) did not have tubes or spurs too narrow for nectarivorous birds (e.g. 1–3 mm wide and long flower tubes typical for plants which are pollinated by butterflies, Mertens et al. 2020); 6) had no nectar guides and; 7) effectively placed pollen on the body of birds during visitation.

Observation of insect–plant interactions, dataset 1

The first dataset was collected during four expeditions between 2016–2018. Animal–plant interactions were collected using security cameras (Vivotek IB8367T with IR night vision; Klomberg et al. 2020). Up to five specimens of each plant species were recorded, each for 24-h of continuous recording, resulting in 1115 individual recordings from 211 plant species. Floral visitors were detected in the video material by either manually searching or using the automatic motion detecting software MotionMeerkat (Weinstein 2015). For calculation of visitor frequency per hour, we included only insect visitors that made contact with plant reproductive organs (similar to Biella et al. 2019). Among a selection of the most common pollinator groups, we found 13 170 insect–plant interactions, with the majority of visits by bees (26.50%; excluding wasps, carpenter bees and honeybees), followed by honeybees (24.84%), hoverflies (15.96%) and moths (10.68%; excluding hawkmoths, for more details on Lepidoptera, Mertens et al. 2021). The data collection prioritized insect–plant interactions, as the cameras were placed close to the plants to enable the identification of insect morphospecies and to record night visitors. Although the dataset includes other types of visitors as well, such as birds or mammals, the sample size was relatively low; too low to consider it robust, particularly for rarer bird–plant interactions. This data was therefore used primarily for insect–flower interactions, later collecting a more complex dataset on bird–flower interactions (dataset 2 below).

Observation of bird–plant interactions, dataset 2

The second dataset was collected between 2018–2020 at the same study sites as dataset 1. The observation unit was a plant individual. For lianas, where the definition of an individual can be complicated, we distinguished flowering parts which were not seemingly connected as separate units. We observed flowering plants that we considered potentially bird-pollinated and met the following criteria: 1) birds had been observed to feed on the flowers during our long-term research on Mt Cameroon or; 2) its nectar volume in a flower covered for 24-h was higher than 0.3 μl/per flower (Chmel et al. unpubl.) and; 3) it flowered at least in three replications along the six transects per study site, or it occurred less frequently within the transects but commonly flowered in the transects vicinity. Bird–plant interactions (visits during which birds fed on nectar) were observed using two complementary methods. The first method was applied for herbs and small shrubs. For their observation, we used the same security cameras to record 10 individuals of each plant species. Each plant individual was recorded for two consecutive days (from 6:00 to 18:00 only). Nevertheless, the total recording times slightly differed for individual plants (Supporting information), because some species were difficult to find, or due to logistic and/or technical problems which sometimes occurred in the harsh weather on Mt Cameroon. Finally, the mean length of the video observation was 152 h per plant species. The recorded floral visitors were identified in the same way as for dataset 1. The second method, conducted simultaneously, was personal observation of trees and larger shrubs, where cameras did not have the capacity to record visits on all flowers at the same time. We aimed to observe eight individuals per plant species, each of them for eight hours equally distributed during the daytime (from 6:00 to 18:00 only). Because we did not find a sufficient number of individuals of some plant species, the mean length of observation was 68 h per species (Supporting information). High trees were usually observed from a neighbouring tree which was climbed using the single rope technique. In total, we recorded 9473 bird–plant interactions in the dataset 2, i.e. occasions where birds fed on nectar, for the four sites during both dry and wet seasons. 22 species of birds were observed feeding on nectar. Sunbirds (Nectarinidae) were the most prominent visitors (12 species, 90.0% of all visits, Supporting information). The observed plants were identified during our long-term research on Mt Cameroon. The taxonomically problematic species were sent to specialists for identification, and voucher specimens were deposited in the Cameroon National Herbarium in Yaounde, Cameroon.

Merging of datasets: comparison of bird and insect visitation frequency

For this part of the study, we considered 88 plant species which occurred in both datasets (Supporting information). The selection was based on the vegetation survey of flowering plants carried out during the collection of the dataset 2. Because both datasets were obtained during different expeditions and by slightly different methodological approaches (see above), we calculated the relative attractiveness of individual plant species for birds and for insects separately. The plants were ranked from the most to least visited species based on bird or insect visitation frequencies (i.e. by the average number of individual visitors per hour of observation). For the purpose of comparing bird and insect visitation, we averaged the visitation frequencies for each plant species that occurred at several sites or flowered during both dry and wet seasons. The plant species with no recorded visits were ranked as zero. Bird visitation frequencies missing in dataset 2 were supplemented from dataset 1 (details in next paragraph). Note that the plants which were observed only in dataset 2 were excluded, as we had no information on insect visits. Nevertheless, none of the excluded plants fit the bird pollination syndrome.

Merging of datasets: individual floral traits as predictors of bird visitation frequency

Although not all plants were observed in dataset 2 (bird–plant interactions), we were able to provide empirical evidence as to whether the omitted plant species were visited by birds or not using dataset 1 (insect–plant interactions). Therefore, we derived the frequencies of bird visits from dataset 1 for 41 plant species that were flowering but omitted during the work on dataset 2. Only one of these plants (*Deinbollia* sp.) was visited by birds (Supporting information), all others showed no visits. By supplementing dataset 2 with dataset 1, we gained detailed information on the bird visitation frequencies (i.e. number of individuals per hour of observation) for 102 plant species in total.

Statistical analysis

To visualise the distribution of plant species within the dimensional space defined by floral traits, we used factor analysis of mixed data (FAMD), a principal component method dedicated to analysing datasets containing both quantitative and qualitative variables (Pagès 2004). The size of the centroids was set to reflect the frequency of bird–plant interactions. For this purpose, the frequencies were averaged for those plant species that occurred at more sites, or during both seasons.

Following the concept model (Fig. 1), a χ^2 contingency test was applied to assess whether the distribution of interactions (bird–plant versus insect–plant) was different from the expected random distribution. This included three separate tests analysing: 1) if the number of common interactions of plants shared by birds and insects (zones II and III in Fig. 1) differed from the number of specific interactions (zones I and IV, Fig. 1); 2) if the plants within the bird pollination syndrome were visited by birds (i.e. occurred in zone I and II, Fig. 1) at a higher rate than expected (i.e. equally distributed across all (I–IV) zones); 3) if the plants within the bird pollination syndrome were visited by birds at a higher rate than by insects (number of interactions within zone I versus zone II, Fig. 1). To analyse whether birds fed mainly on ornithophilous plants (Fig. 1C), we applied the Wilcoxon test and compared the mean ranks of visitation frequency between the ornithophilous and non-ornithophilous plants.

We used compound Poisson generalized linear mixed model (CPGLMM) (Zhang 2013) to assess the effect of floral resource quantity and individual floral traits (fixed effects) on bird visitation frequencies. The CPGLMM method was also capable of handling our zero inflated data. To account for the potential spatiotemporal patterns and abundance of flowering plants in our dataset, we set the site, season and abundance of flowering plants per hectare as random effects. For the plants which were relatively common at the study site but did not flower on the transects, we arbitrarily set their abundance as one individual per two hectares. For individual floral traits, we analysed the conditional effect, i.e. the effect of each floral trait was tested within a full model (six traits) against a model containing all floral traits less the one being tested (five traits). Additionally, we computed the marginal R^2 (explained variation) from the CPLGLMM models following Nakagawa et al. (2017). This, together with the model parsimony (AIC), allowed us to compare the relative effect of resource quantity and the set of floral traits in relation to the bird visitation frequencies.

Results

Bird visitors were observed feeding on 48 plant species. Nine of these plant species fit the bird pollination syndrome (Fig. 2A–I). Overall, the studied plant species expressed a wide diversity of flowers with substantial differences in the composition of individual floral traits (Fig. 3).

The plants were evenly distributed in the bird–plant × insect–plant interaction space (χ^2 test, $df_{44,44} = 1$, $\chi^2 = 0$, $p = 1.000$), whilst half (21) out of the 42 plant species visited by birds had a larger proportion of bird to insect rank visitation (Fig. 4, upper left quadrant). The other half of the plant species were similarly important for both bird and insect visitors (Fig. 4, upper right quadrant). The ornithophilous plants occurred in the bird-favoured area (i.e. zones I and II in Fig. 1) more often than expected by chance (χ^2 test, $df_{9,0} = 1$, $\chi^2 = 9.00$, $p = 0.003$) (Fig. 4). They hosted a larger proportion of bird to insect rank visitation, but only marginally, i.e. visits occurred within the bird–plant interaction zone (zone I in Fig. 1) at the higher rate than expected by chance (χ^2 test,

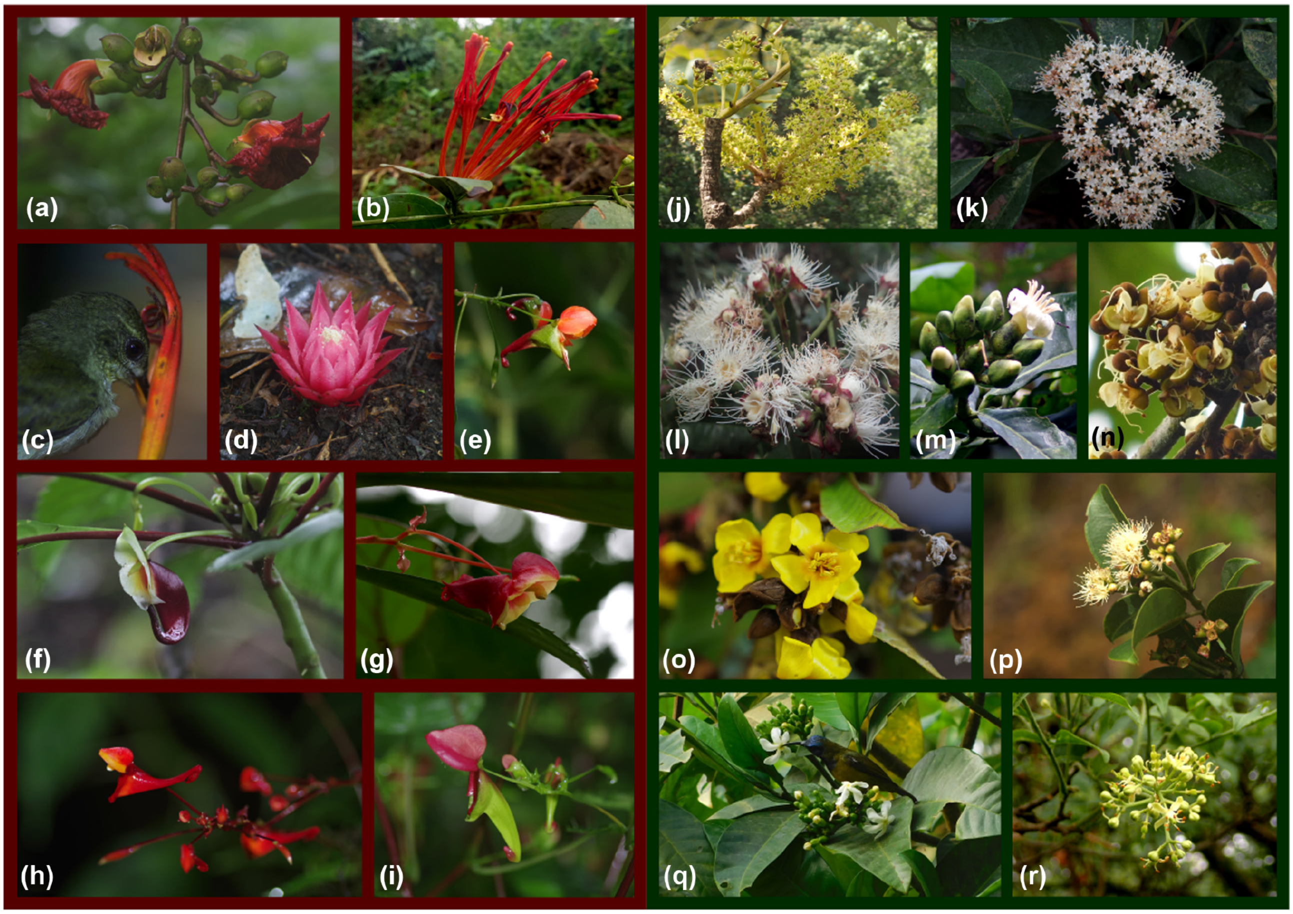
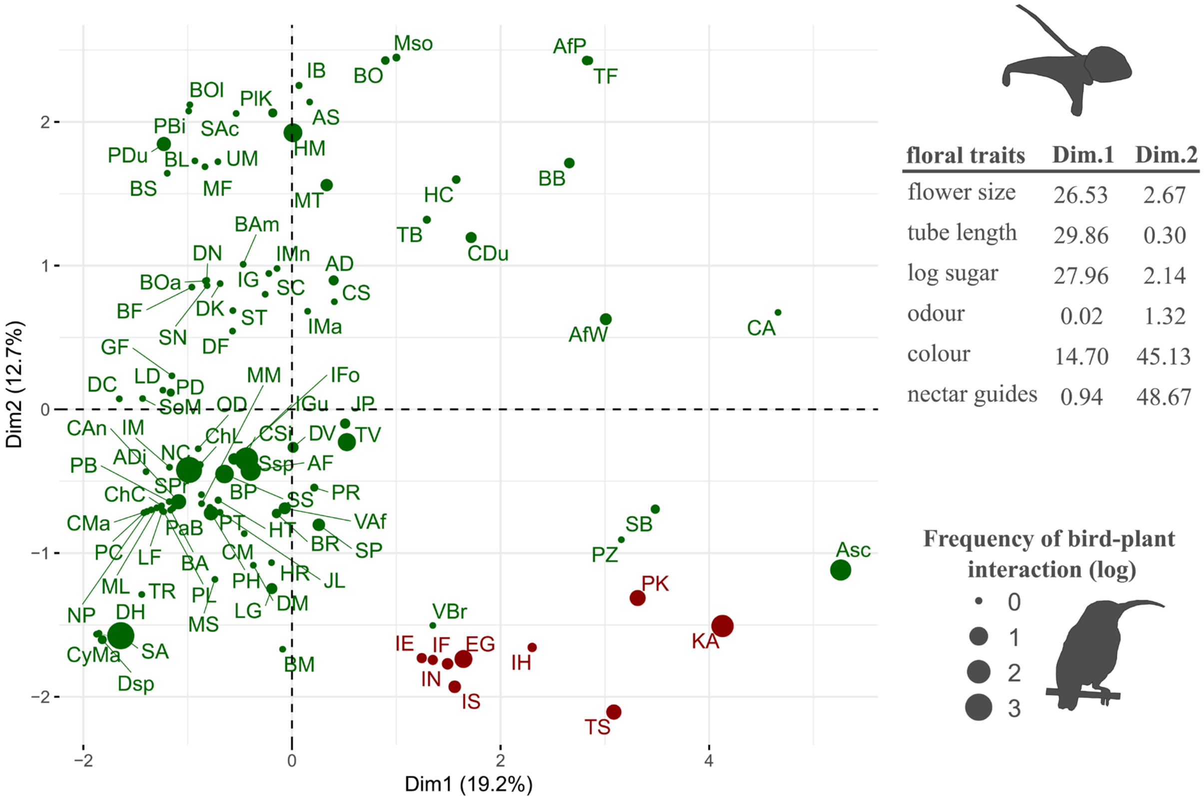


Figure 2. Flowers of the nine ornithophilous (a–i, left red blocks) and nine most visited non-ornithophilous (j–r, right green blocks) plant species. Both ornithophilous and non-ornithophilous plants are ordered by decreasing frequency of bird–plant interaction. (a) *Kigelia africana*, (b): *Englerina gabonensis*, (c) *Phragmathera kamerunensis*, (d) *Thonningia sanguinea*, (e) *Impatiens sakeriana*, (f) *Impatiens niamniamensis*, (g) *Impatiens etindensis*, (h) *Impatiens frithii*, (i) *Impatiens hians*, (j) *Shefflera abyssinica*, (k) *Nuxia congesta*, (l) *Syzygium sp*, (m) *Anthocleista scandens*, (n) *Anthonotha fragrans*, (o) *Hugonia micans*, (p) *Syzygium staudtii*, (q) *Tabernemontana ventricosa*, (r) *Clausena anisata*. Photographs were provided by the authors.



floral traits	Dim.1	Dim.2
flower size	26.53	2.67
tube length	29.86	0.30
log sugar	27.96	2.14
odour	0.02	1.32
colour	14.70	45.13
nectar guides	0.94	48.67

Figure 3. Ordination diagram (FAMD) showing the distribution of 102 plant species (red = ornithophilous plant species, green = other plant species) within the morpho-space defined by the composition of six floral traits: colour, odour, presence of nectar guides, size, tube length and log sugar content per flower. Point size designates the frequency of bird visitors (on a logarithmic scale). The first (dim1) and second (dim2) axes explained 19.2% and 12.7% of the variation, respectively. Contributions (%) of individual explanatory variables to the explained variation by dim1 and dim2 are shown next to the diagram. Species codes: AD, *Acanthopale decempedalis*; Adi, *Anchomanes difformis*; AF, *Anthonotha fragrans*; AfP, *Aframomum* sp purple; AfW, *Aframomum* sp white; AS, *Acanthonema strigosum*; Asc, *Anthocleista scandens*; BA, *Basella alba*; BAm, *Begonia ampla*; BB, *Berlinia bracteosa*; BF, *Begonia fusialata*; BL, *Begonia letouzeyi*; BM, *Begonia mannii*; BO, *Brillantaisia owariensis*; BOa, *Begonia oxyanthera*; BOl, *Begonia oxyloba*; BP, *Begonia poculifera*; BR, *Bertiera racemosa*; BS, *Begonia scutifolia*; CA, *Calochone acuminate*; CAn, *Clausena anisata*; Cdu, *Costus dubius*; CM, *Crassocephalum montuosum*; CMa, *Culcasia mannii*; CS, *Calanthe sylvatica*; Csi, *Clerodendrum silvanum*; CyMa, *Cyphostemma mannii*; DC, *Dioscoreophyllum cumminsii*; DF, *Distephanus biafrae*; DH, *Discocloaxylon hexandrum*; DK, *Disperis kamerunensis*; DM, *Dorstenia mannii*; DN, *Disperis nitida*; Dsp, *Deinbollia* sp 1; DV, *Dicranolepis vestita*; EG, *Englerina gabonensis*; GF, *Gomphia flava*; HC, *Heinsia crinite*; HM, *Hugonia micans*; HR, *Hylodesmum repandum*; HT, *Hypoestes triflora*; ChC, *Chlorophytum comosum*; ChL, *Chassalia laikomensis*; IB, *Impatiens burtonii*; IE, *Impatiens etindensis*; IF, *Impatiens frithii*; IFo, *Ixora foliosa*; IG, *Isoglossa glandulifera*; IGu, *Ixora guineensis*; IH, *Impatiens hians*; IM, *Ilex mitis*; IMa, *Impatiens macroptera*; Imn, *Impatiens mannii*; IN, *Impatiens niamniamensis*; IS, *Impatiens sakeriana*; JL, *Justicia laxa*; JP, *Jasminum preussii*; KA, *Kigelia Africana*; LD, *Liparis deistelii*; LF, *Laccodiscus ferrugineus*; LG, *Leea guineensis*; MF, *Momordica foetida*; ML, *Maesa lanceolata*; MM, *Marantochloa monophylla*; MS, *Melanthera scandens*; Mso, *Mimulopsis solmsii*; MT, *Mussaenda tenuiflora*; NC, *Nuxia congesta*; NP, *Nephthytis poissonii*; OD, *Oncoba dentate*; PaB, *Psychotria bifaria*; PB, *Palisota barteri*; PBi, *Polystachia bicalcarata*; PC, *Piper capense*; PD, *Plectranthus decurrens*; PDu, *Psydrax dunlapii*; PH, *Psychotria hypsophila*; PK, *Phragmanthera kamerunensis*; PL, *Psychotria leptophylla*; PlK, *Plectranthus kamerunensis*; PR, *Pavetta rigida*; PT, *Psychotria thonneri*; PZ, *Pararistolochia zenkeri*; SA, *Schefflera abyssinica*; SAc, *Stachys aculeolata*; SB, *Sherbournia bignoniiflora*; SC, *Sabicea calycina*; SN, *Solanum nigrum*; SoM, *Solanecio mannii*; SP, *Sabicea pilosa*; SPr, *Spermacoce princeae*; SS, *Syzygium staudtii*; Ssp, *Syzygium* sp.; ST, *Solanum terminale* subsp *inconstans*; TB, *Tabernaemontana brachyantha*; TF, *Thunbergia fasciculate*; TR, *Trichilia rubescens*; TS, *Thonningia sanguinea*; TV, *Tabernemontana ventricosa*; UM, *Utricularia mannii*; VAf, *Voacanga Africana*; VBr, *Voacanga bracteata*.

$df_{7,2} = 1$, $\chi^2 = 2.77$, $p = 0.096$) (Fig. 4). However, the ornithophilous plants did not see higher frequencies of bird visits when compared with the other bird-visited plants visited by birds (Wilcoxon test, $df_{9,39} = 1$, $W = 120$, $p = 0.146$) (e.g. Fig. 2j–r). Altogether, plants visited by birds did not occupy a unique portion of the trait space, i.e. we did not observe a distinct separation between the visited and non-visited plants in terms of the composition of their floral traits (Fig. 3).

Although birds did not appear to prefer flowers of a specific phenotype, the floral traits still explained a relatively high proportion of variability in the frequency of bird–plant interactions ($R^2 = 0.2132$). A comparable proportion

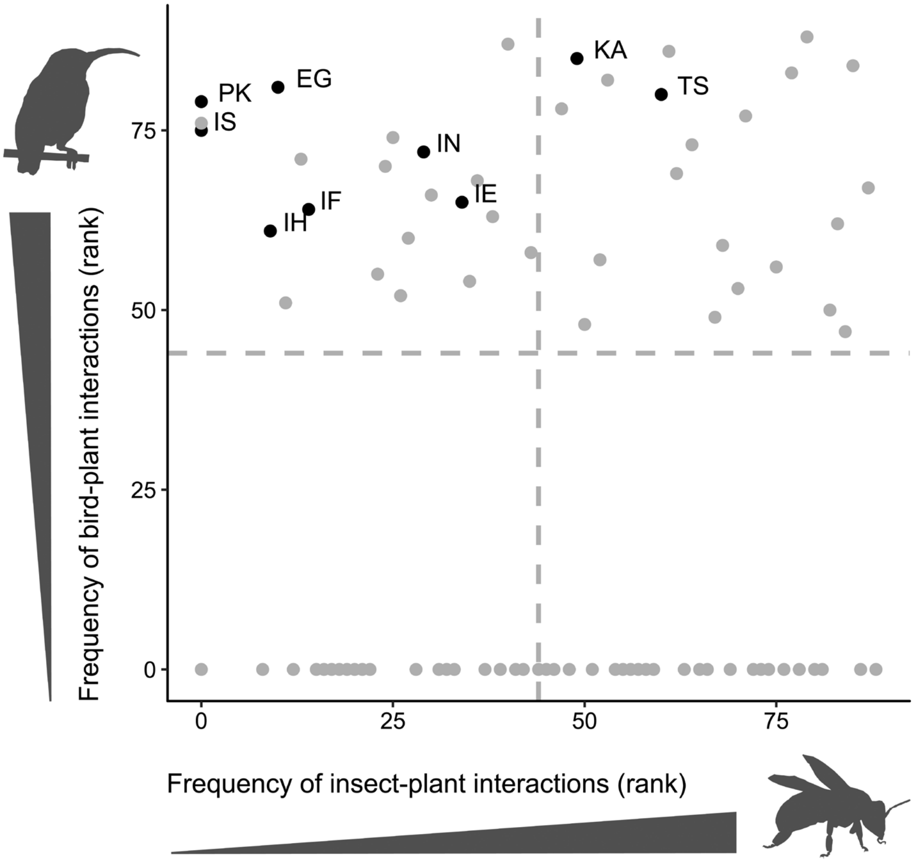


Figure 4. Relationship between ranked bird and insect frequencies at 88 different plant species. Plant species fitting the bird pollination syndrome (EG, *Englerina gabonensis*; IE, *Impatiens etindensis*; IF, *Impatiens frithii*; IH, *Impatiens hians*; IN, *Impatiens niamniamensis*; IS, *Impatiens sakeriana*; KA, *Kigelia Africana*; PK, *Phragmanthera kamerunensis*; TS, *Thonningia sanguinea*) are visualised in black, the rest in grey.

was explained by the quantity of nectar resource offered by an individual of a plant species ($R^2 = 0.2076$). However, the resource quantity itself explained more variability in the visitation frequencies than any other floral trait. Moreover, in terms of the model parsimony (AIC), the resource quantity was a better predictor, with a positive effect on the visitation frequency (Table 1, Fig. 5). Among the individual floral traits: odour, sugar content, tube length, and presence/absence of nectar guides were significant predictors of visitation frequency (ordered by decreasing amount of explained variability) (Table 1). On the contrary, the visitation frequency was not affected by the floral colour and size (Table 1). The frequency of bird visits tended to be higher on flowers that exuded odour, with an increased sugar content, with a longer tube length, and with the absence of nectar guides (Table 1).

Table 1. Influence of individual plant traits on bird visitor frequency.

Model	R^2 Marginal	AIC	χ^2	p	Direction of relationship
~Zero model	0.0000	263.38			
~Resource quantity	0.2076	159.03	106.34	**<0.001**	++
~Floral traits	0.2132	211.35	64.03	**<0.001**	
Contribution of individual floral traits					
Odour	0.0957	-	22.66	**<0.001**	Exude odour ++
Sugar content	0.0333	-	23.78	**<0.001**	++
Tube length	0.0284	-	4.70	**0.030**	++
Nectar guides	0.0146	-	4.61	**0.031**	Absent ++
Colour	0.0032	-	0.62	0.430	n.s.
Flower size	0.0014	-	0.29	0.590	n.s.

CPGLMM, n = 184, elevation and season were set as random effects. Models ordered by marginal R^2. Colour was tested as a two-level factor: orange-red versus other colours. We indicate the direction of significant relationships ($p < 0.05$ in bold) with bird frequency, where ++ = positive for continuous variables while the factor with highest value of bird frequency is shown for qualitative variables.

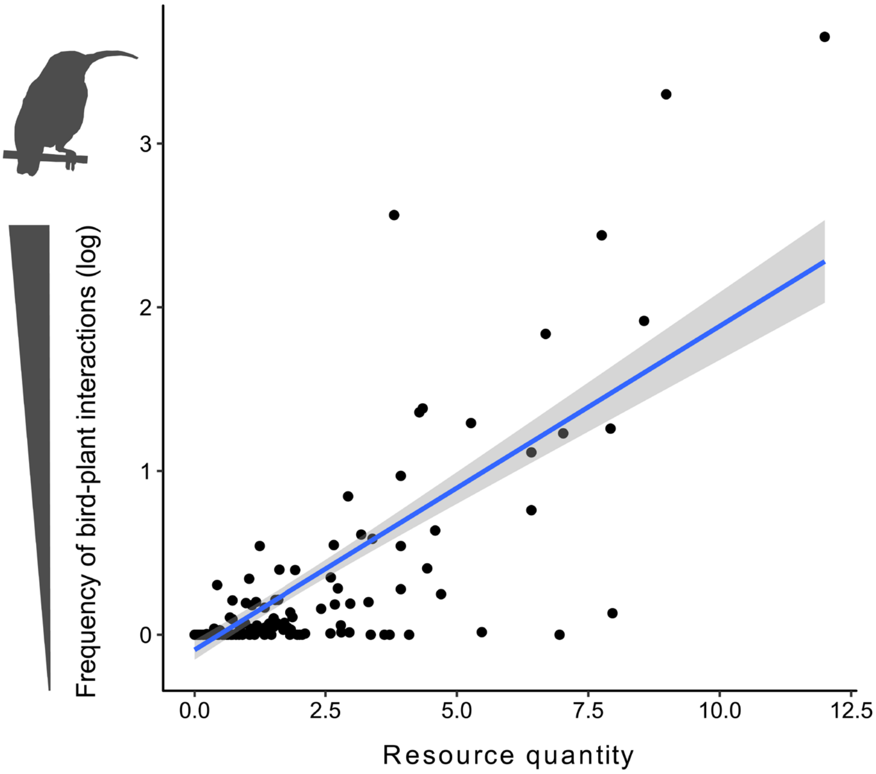


Figure 5. Relationship between bird visitation frequency and resource quantity (nectar sugar production per average plant individual). Shaded area represents the standard error. Logarithmic transformation was used for both variables.

Discussion

Plants evenly occupy the insect–plant × bird–plant interaction space

We documented a regular distribution of plants in the four zones of niche space delimited by bird–plant and insect–plant interaction axes. Based on the conceptual model, an equal proportion of plants tended to be specialised either to birds or insects (i.e plants in zones I and IV in the conceptual model) and the same proportion consisted of generalized plants, where the ranked interaction frequencies of both visitor groups overlapped (zones II and III). This pattern therefore partly showed the high diversification of pollination niches (Johnson 2010), and partly supported the ideas of Waser et al. (1996) and Ollerton et al. (2009) who underlined that a relatively large proportion of flowers do not host a specific pollinator. Nevertheless, we should also consider that the degree of specialization and the ability of pollination syndromes to predict pollinators can differ in individual floras (Johnson and Wester 2017), as well as under different environmental conditions (Klomberg et al. 2020). This could also be the reason why we did not find consistent support (or consistent rejection) of the pollination syndrome concept (Rosas-Guerrero et al. 2014, Wang, X. et al. 2020). Although we observed similar numbers of plants in the four zones of our conceptual framework, the regularity of the plant distribution in the bird non-preferred zones (i.e. zones III and IV in Fig. 1) was somewhat disrupted by the fact that these plants were not visited by birds at all. We assume that there is a plant profitability threshold, which makes these plants unattractive for birds. Conversely, we found only three plant species that are exclusively visited by birds with no records of insect visitors (*Impatiens sakeriana, Phragmanthera kamerunensis, Sabicea pilosa*). We propose two primary explanations for why ornithophilous plants are still at least somewhat attractive for insects (Wilson et al. 2004): 1) plants adapted to birds usually produce a lot of nectar, which, despite other anti-insect adaptations, acts as a strong attractant; 2) flowers also offer other insect rewards, such as pollen.

Validity of the bird pollination syndrome

Our results showed that the set of floral traits used to represent the bird pollination syndrome (Faegri and van der Pijl 1979, Fenster et al. 2004, Cronk and Ojeda 2008) are indeed indicative of specialisation towards bird pollination. Ornithophilous plant species were visited by birds at higher rates than by chance alone, and were preferred by birds more so than insects . There were two exceptions to this, *Kigelia africana* and *Thonningia sanguinea*, which, despite having the bird pollination syndrome, were also favoured by insects. This aligns with studies from other regions showing that these plants can be pollinated by a wider spectrum of pollinator groups. When considering additional floral traits, e.g. a wide floral tube of *Kigelia africana* or a geoflory of *Thonningia sanguinea*, these species did not fit the bird pollination syndrome perfectly (Quintero et al. 2017, Namah et al. 2019). While Namah et al. (2019) also described common interactions of *Kigelia africana* with birds and insects, other studies demonstrated *K. africana* was primarily pollinated by fruit bats (Baker 1961, Ayensu 1974). The pollination system of *Thonningia sanguinea* is similarly ambivalent, as both flies (Goto et al. 2012) and birds (Quintero et al. 2017) were documented as its main pollinators. The other ornitophilous plants, which were affiliated only to the bird–plant interaction zone, were shown to be bird pollinated in other studies (Bartoš and Janeček 2014, Janeček et al. 2011, 2015).

Regardless of any minor irregularities mentioned above, our study supports the validity of the bird pollination syndrome hypothesis. Hence, it is another example demonstrating that reddish tubular flowers with copious nectar reward are not a form of adaptation exclusive to the most studied nectar specialist – New World's hummingbirds (e.g. Dziedzioch et al. 2003, Muchhala 2006), but such traits represent a convergent evolutionary shift to other specialised groups of birds such as sunbirds (Rodríguez-Gironés and Santamaría 2004, Fleming and Muchhala 2008). Nevertheless, the representation of ornithophilous plant species in Afrotropical rainforests appears to be much lower compared to the Neotropics. In the Neotropics, the interactions with birds (hummingbirds) may have accelerated an extensive speciation in species rich families, e.g. Bromeliaceae (Givnish et al. 2014, Kessler et al. 2020). Stiles (1985) documented 50 plant species pollinated primarily by hummingbirds in a Costa Rican submontane forest. In a montane forest in the Andes, Dziedzioch et al. (2003) observed hummingbirds feeding on 67 plant species half of which had red tubular flowers. In the Atlantic Forest, including lowland and highland sites, Buzato et al. (2000) documented 86 hummingbird-pollinated plant species. Nevertheless, here only nine out of the 42 studied plants bore the characteristics typical of ornithophilous flowers.

Effectiveness of birds as pollinators

It is important to acknowledge that, from the plant's perspective, the interaction frequency is not the only parameter determining pollinator effectiveness, and that this can in fact be much higher in specialised plants because of various floral adaptations (Thomson et al. 2000, Hargreaves et al. 2004). Birds have been shown to be highly effective pollinators, even during just a single visitation to the ornithophilous plant *Impatiens sakeriana* (Janeček et al. 2011). For example, the effectiveness can be increased by different mechanisms allowing specific and precise pollen placement on parts of the bird body (Bartoš and Janeček 2014). Such placement prevents heterospecific pollen deposition on stigmas (Morales and Traveset 2008). Ornithophilous plants do not necessarily need to receive many visits, but rather simply a few effective ones in order to reproduce.

Birds can likely also act as effective pollinators on numerous non-ornithophilous plants. For example, even if individual flowers were very small (e.g. *Nuxia congesta* or *Syzigium* sp., Fig. 2k–l) birds that perched directly on the inflorescences will likely transfer pollen with their feet or other body parts as shown in a recent study of a montane system in Nigeria (Nsor et at. 2019).

On the other hand, we are aware that not all visitors attracted to flowers act as pollinators. We witnessed how some birds participated in nectar robbing, i.e. removing nectar without contacting the anthers and/or stigma (reviewed by Irwin et al. 2010). Although we were not able to quantify the proportion of nectar robbing for individual plant species, we did not observe exclusive nectar thieving for any plant species. Therefore, in many cases, the simple visitation rate likely does not reflect the pollination effectiveness, measured for example as germinated pollen load per visit (Rocca and Sazima 2013). Here we focused primarily on the visitor perspective, i.e. what defines the attractiveness of a plant and floral choice. At this level, the effectiveness of pollination is not so important, although it would be extremely valuable to unravel the relationship between the visitation rate and the pollination effectiveness in individual plant species.

Birds feed both on ornithophilous and non-ornithophilous plants

Although all studied ornithophilous plants hosted bird visitors, birds also fed frequently on other non-ornithophilous plants. Moreover, their interaction frequencies on these non-ornithophilous plants were not significantly different from the specialised ornithophilous plants. This finding corresponds with the observation that bird adaptations, such as a long bill and tongue, enable drinking from specialised tubular flowers, but they do not prevent them from also using flowers with more exposed nectar (Janeček et al. 2007, 2012). These results agree with other studies showing that phenotypically nonspecialised plants are important in the nutrition of sunbirds (Nsor et al. 2019), but also hummingbirds (Maruyama et al. 2013) or honeyeaters (Castro and Robertson 1997). Nevertheless, hummingbirds are expected to have the closest relationship with ornithophilous plants fitting to the bird pollination syndrome (Fleming and Muchhala 2008). Given this, similar studies from the New World are needed to explore the wider validity of observed patterns.

It is therefore evident that birds care little about whether they feed from ornithophilous or non-ornithophilous flowers, but we should avoid the interpretation that ornithophilous plants are generally an unimportant source of nectar. They can be a crucial nectar source in some periods of the year (e.g. wet season; Klomberg et al. 2020) or for some sunbird species (Janeček et al. 2015, Janeček et al. unpubl.)

Resource quantity as the best predictor of floral choice

Our findings support those of other studies which suggest floral choice is governed primarily by profitability – the amount and availability of nectar reward (Pleasants and Waser 1985, Collins and Newland 1986, Schmid et al. 2016). Although the nectar production per plant appeared to be the most important trait for nectarivorous birds, additional floral traits were also at play. Some plant species may produce a large quantity of nectar per plant individual which would potentially attract bird visitors, but this resource may be inaccessible for them (Grant and Temeles 1992). For instance, nectar containing floral tubes are likely too narrow for a bird's beak in few of the sampled species (e.g. *Heinsia crinita* or *Impatiens mannii*). In other cases, plants may produce a large total quantity of nectar but in super abundant small stellate flowers with a very low amount of nectar per flower (e.g. *Ilex mitis*), thus making the handling of flowers unprofitable for birds. On the contrary, some plant traits that have evolved to attract other pollinator groups did not deter birds. We found that the frequency of birds tended to be higher on flowers that exert odour, even though this trait plays a prominent role in the locating of flowers, especially for nocturnal bats and moths (Faegri and van den Pijl 1979). The colour of flowers did not influence the frequency of feeding birds, suggesting that bird floral choice is mainly based on previous experience, during which birds tested how much nectar the plant offers and whether it is accessible, rather than on a priori visual cues of the flowers (Wolf and Heinsworth 1983). Our results indirectly support the theory that some floral traits did not evolve as an adaptation to attract birds but rather to deter insects. This seems to be true not only for red colouration, which is less conspicuous for bees (Lunau et al. 2011, Bergamo et al. 2016, Coimbra 2019), but also for some other traits, e.g. the tube length which is generally considered as a trait excluding visitors with the short mouthparts (Vlašánková et al. 2017, Coimbra 2019).

Finally, we are aware that floral choice will also be affected by competition and resource partitioning. This may prevent birds from visiting the seemingly richest nectar resource and may account for some of the unexplained variation in bird visitation rates. Here we assume that there is no difference in flowering plant preference between bird visitors, however resource partitioning is generally common within nectarivorous bird communities where smaller species are often forced to forage on less productive plants (Gill and Wolf 1977, Ford and Paton 1982, Janeček et al. 2012), while intraspecific differences in foraging patterns have been also described (Dupont et al. 2014, Maruyama et al. 2016).

Conclusions

This analysis of flower–visitor interactions on Mt Cameroon revealed that while nectarivorous birds often visited specialised ornithophilous plants characterised by the bird pollination syndrome, these birds also fed frequently on other unspecialised plants. From a bird's perspective, the attractiveness of each plant is defined primarily by the nectar resource on offer. Nectar reward appears to be a better predictor of bird visitation than other floral traits traditionally related to the bird pollination syndrome.

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Author contributions

Kryštof Chmel: Data curation (equal); Formal analysis (equal); Methodology (equal); Visualization; (equal); Writing – original draft (equal); Writing – review and editing (equal). **Francis Ewome**: Data curation (equal); Writing – review and editing (supporting). **Guillermo Gómez**: Data curation (equal); Writing – review and editing (equal). **Yannick Klomberg**: Data curation (equal); Formal analysis (equal); Writing – review and editing (equal). **Jan E. J. Mertens**: Data curation (equal); Formal analysis (equal); Writing – review and editing (equal). **Robert Tropek**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Writing – review and editing (equal). **Stepan Janecek**: Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.xsj3tx9ff> (Chmel et al. 2021).

References

Aguilar-Rodríguez, P.A. et al. 2016. From dusk till dawn: nocturnal and diurnal pollination in the epiphyte *Tillandsia heterophylla* (Bromeliaceae). – Plant Biol. 18: 37–45.

Araujo, A. C. and Sazima, M. 2003. The assemblage of flowers visited by hummingbirds in the 'capões' of southern Pantanal, Mato Grosso do Sul, Brazil. – Flora 198: 427–435.

Ashworth, L. et al. 2015. Pollination syndromes: a global pattern of convergent evolution driven by the most effective pollinator. – In: Pontarotti, P. (ed.), Evolutionary biology: biodiversification from genotype to phenotype. – Springer, pp. 203–224.

Ayensu, E. S. 1974. Plant and bat interactions in West Africa. – Ann. Miss. Bot. Gard. 61: 702–727.

Baker, H. G. 1961. The adaptation of flowering plants to nocturnal and crepuscular pollinators. – Q. Rev. Biol. 36: 64–73.

Bartoš, M. and Janeček, Š. 2014. Pollinator-induced twisting of flowers sidesteps floral architecture constraints. – Curr. Biol. 24: R793–R795.

Bartoš, M. et al. 2012. Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: a comparison with six other co-flowering species. – S. Afr. J. Bot. 78: 63–74.

Bawa, K. 1990. Plant–pollinator interactions in tropical rain forests. – Annu. Rev. Ecol. Syst. 21: 399–422.

Bergamo, P. J. et al. 2016. Flower colour and visitation rates of *Costus arabicus* support the 'bee avoidance' hypothesis for red-reflecting hummingbird-pollinated flowers. – Funct. Ecol. 30: 710–720.

Biella, P. et al. 2019. Experimental loss of generalist plants reveals alterations in plant–pollinator interactions and a constrained flexibility of foraging. – Sci. Rep. 9: 1–13.

Brown, E. D. and Hopkins, M. J. G. 1995. A test of pollinator specificity and morphological convergence between nectarivorous birds and rainforest tree flowers in New Guinea. – Oecologia 103: 89–100.

Buzato, S. et al. 2000. Hummingbird-pollinated floras at three Atlantic forest sites. – Biotropica 32: 824–841.

Cable, S. and Cheek, M. 1998. Plants of Mount Cameroon: a conservation checklist. – R. Bot. Gard.

Castro, I. and Robertson, A. 1997. Honeyeaters and the New Zealand forest flora: the utilisation and profitability of small flowers. – N. Z. J. Ecol. 21: 169–179.

Chlumská, Z. et al. 2014. How to preserve plant samples for carbohydrate analysis? Test of suitable methods applicable in remote areas. – Folia Geobot. 49: 1–15.

Chmel, K. et al. 2021. Data from: Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective. – Dryad, <http://dx.doi.org/10.5061/dryad.xsj3tx9ff>.

Coimbra, G. et al. 2020. Flower conspicuousness to bees across pollination systems: a generalized test of the bee-avoidance hypothesis. – Front. Plant Sci. 11: 558684.

Collias, N. E. and Collias, E. C. 1968. Anna´s hummingbirds trained to select different colors in feeding. – Condor 70: 273–274.

Collins, B. G. and Newland, C. 1986. Honeyeater population changes in relation to food availability in the Jarrah forest of Western Australia. – Austral Ecol. 11: 63–76.

Cronk, Q. and Ojeda, I. 2008. Bird-pollinated flowers in an evolutionary and molecular context. – J. Exp. Bot. 59: 715–727.

Dalsgaard, B. et al. 2011. Specialization in plant–hummingbird networks is associated with species richness, contemporary precipitation and quaternary climate-change velocity. – PLoS One 6: e25891.

Darwin, C. 1862. On the various contrivances by which British and foreign orchids are fertilized. – John Murray.

Dellinger, A. S. 2020. Pollination syndromes in the 21st century: where do we stand and where may we go? – New Phytol. 228: 1193–1213.

Dupont, Y. L. et al. 2014. Spatial structure of an individual-based plant–pollinator network. – Oikos 123: 1301–1310.

Dziedzioch, C. et al. 2003. The hummingbird plant community of a tropical montane rain forest in southern Ecuador. – Plant Biol. 5: 331–337.

Essenberg, C. J. 2012. Explaining variation in the effect of floral density on pollinator visitation. – Am. Nat. 180: 153–166.

Faegri, K. and van der Pijl, L. 1979. The principles of pollination ecology. – Elsevier.

Fenster, C. B. et al. 2004. Pollination syndromes and floral specialization. – Annu. Rev. Ecol. Evol. Syst. 35: 375–403.

Fenster, C. B. et al. 2015. Quantifying hummingbird preference for floral trait combinations: the role of selection on trait interactions in the evolution of pollination syndromes. – Evolution. 69: 1113–1127.

Fleming, T. H. and Muchhala, N. 2008. Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. – J. Biogeogr. 35: 764–780.

Ford, H. A. and Paton, D. C. 1982. Partitioning of nectar sources in an Australian honeyeater community. – Austral Ecol. 7: 149–159.

Freitas, L. et al. 2006. Pollination by hummingbirds and bees in eight syntopic species and a putative hybrid of Ericaceae in southeastern Brazil. – Plant Syst. Evol. 258: 49–61.

Galen, C. 2000. High and dry: drought stress, sex-allocation trade-offs, and selection on flower size in the alpine wildflower *Polemonium viscosum*. – Am. Nat. 156: 72–83.

Gill, F. B. and Wolf, L. L. 1975. Foraging strategies and energetics of East African sunbirds at mistletoe flowers. – Am. Nat. 109: 491–510.

Gill, F. B. and Wolf, L. L. 1977. Nonrandom foraging by sunbirds in a patchy environment. – Ecology 58: 1284–1296.

Givnish, T. J. et al. 2014. Adaptive radiation, correlated and contingent evolution, and net species diversification in Bromeliaceae. – Mol. Phylogenet. Evol. 71: 55–78.

Goto, R. et al. 2012. A novel brood-site pollination mutualism: the root holoparasite *Thonningia sanguinea* (Balanophoraceae) and an inflorescence-feeding fly in the tropical rainforests of West Africa. – Plant Species Biol. 27: 164–169.

Grant, V. and Temeles, E. J. 1992. Foraging ability of rufous hummingbirds on hummingbird flowers and hawkmoth flowers. – Proc. Natl Acad. Sci. USA 89: 9400–9404.

Krömer, T. et al. 2006. Distribution and flowering ecology of bromeliads along two climatically contrasting elevational transects in the Bolivian Andes. – Biotropica 38: 183–195.

Hargreaves, A. L. et al. 2004. Do floral syndromes predict specialization in plant pollination systems? An experimental test in an 'ornithophilous' African Protea. – Oecologia 140: 295–301.

Herrera, C. M. 1996. Floral traits and plant adaptation to insect pollinators: a devil's advocate approach. – In: Floral biology. Springer, pp. 65–87.

Irwin, R. E. et al. 2010. Nectar robbing: ecological and evolutionary perspectives. – Annu. Rev. Ecol. Evol. Syst. 41: 271–292.

Janeček, Š. et al. 2007. Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa. – Afr. J. Ecol. 45: 607–613.

Janeček, Š. et al. 2011. Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? – Oikos 120: 178–183.

Janeček, Š. et al. 2012. Food selection by avian floral visitors: an important aspect of plant-flower visitor interactions in West Africa. – Biol. J. Linn. Soc. 107: 355–367.

Janeček, Š. et al. 2015. Convergent evolution of sunbird pollination systems of Impatiens species in tropical Africa and hummingbird systems of the New World. – Biol. J. Linn. Soc. 115: 127–133.

Johnson, S. D. 2010. The pollination niche and its role in the diversification and maintenance of the southern African flora. – Phil. Trans. R. Soc. B 365: 499–516.

Johnson, S.D. and Wester, P. 2017. Stefan Vogel's analysis of floral syndromes in the South African flora: an appraisal based on 60 years of pollination studies. – Flora 232: 200–206.

Kessler, M. et al. 2020. The role of hummingbirds in the evolution and diversification of Bromeliaceae: unsupported claims and untested hypotheses. – Bot. J. Linn. Soc. 192: 592–608.

Klomberg et al. 2020. Spatiotemporal shifts in the role of floral traits in shaping tropical plant-pollinator interactions. – bioRxiv. doi: 10.1101/2020.10.16.342386.

Lefevre, R. 1967. Aspect de la pluviométrie dans la région du Mont Cameroun. – Cah. ORSTOM. Série Hydrol. 4: 15–44.

Lunau, K. et al. 2011. Avoidance of achromatic colours by bees provides a private niche for hummingbirds. – J. Exp. Biol. 214: 1607–1612.

Maicher, V. et al. 2020. Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. – J. Biogeogr. 47: 342–354.

Maruyama, P. K. et al. 2013. Pollination syndromes ignored: importance of non-ornithophilous flowers to Neotropical savanna hummingbirds. – Naturwissenschaften 100: 1061–1068.

Maruyama, P. K. et al. 2016. Does intraspecific behavioural variation of pollinator species influence pollination? A quantitative study with hummingbirds and a Neotropical shrub. – Plant Biol. 18: 913–919.

Mertens et al. 2020. Changes in pollinator community of *Scadoxus cinnabarinus* (Amaryllidaceae) along its elevational range on Mount Cameroon. – Arthropod–Plant Interact.14: 215–226.

Mertens et al. 2021. Elevational and seasonal patterns of butterflies and hawkmoths in plant–pollinator networks in tropical rainforests of Mt Cameroon. – Sci. Rep. 11: 9710.

Morales, C. L. and Traveset, A. 2008. Critical reviews in plant sciences interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness interspecific pollen transfer: magnitude, prevalence and consequences for plant fitness. – CRC Crit. Rev. Plant Sci. 27: 221–238.

Miller, R.S. and Miller, R.E. 1971. Feeding activity and color preference of ruby-throated hummingbirds. – Condor 73: 309–313.

Muchhala, N. 2006. The pollination biology of *Burmeistera* (Campanulaceae): specialization and syndromes. – Am. J. Bot. 93: 1081–1089.

Nakagawa, S. et al. 2017. The coefficient of determination R^2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. – J. R. Soc. Interface 14: 20170213.

Namah, J. et al. 2019. Reproductive biology of the sausage tree (*Kigelia africana*) in kruger National Park, South Africa. – Koedoe 61: 1–7.

Nsor, C. A. et al. 2019. Promiscuous pollinators—evidence from an Afromontane sunbird–plant pollen transport network. – Biotropica 51: 538–548.

Ollerton, J. et al. 2009. A global test of the pollination syndrome hypothesis. – Ann. Bot. 103: 1471–1480.

Ollerton, J. et al. 2011. How many flowering plants are pollinated by animals? – Oikos 120: 321–326.

Padyšáková, E. et al. 2013. Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae). – PLoS One 8: e59299.

Pagès, J. 2004. Analyse factorielle de donnees mixtes: principe et exemple d'application. – Montpellier SupAgro, <www. agro-montpellier. fr/sfds/CD/textes/pages1.pdf> in press.

Partida-Lara, R. et al. 2018. Pollination syndromes and interaction networks in hummingbird assemblages in El Triunfo Biosphere Reserve, Chiapas, Mexico. – J. Trop. Ecol. 34: 293–307.

Pleasants, J. M. and Waser, N. M. 1985. Bumblebee foraging at a 'hummingbird' flower: reward economics and floral choice. – Am. Midl. Nat. 114: 283–291.

Proctor, M. et al. 1996. The natural history of pollination. – HarperCollins Publishers.

Quintero, E. et al. 2017. Sunbird surprise: a test of the predictive power of the syndrome concept. – Flora Morphol. Distrib. Funct. Ecol. Plants 232: 22–29.

Rocca, M. A. and Sazima, M. 2006. The dioecious, sphingophilous species *Citharexylum myrianthum* (Verbenaceae): pollination and visitor diversity. – Flora Morphol. Distrib. Funct. Ecol. Plants 201: 440–450.

Rocca, M. A. and Sazima, M. 2013. Quantity versus quality: identifying the most effective pollinators of the hummingbird-pollinated *Vriesea rodigasiana* (Bromeliaceae). – Plant Syst. Evol. 299: 97–105.

Rodríguez-Gironés, M. A. and Santamaría, L. 2004. Why are so many bird flowers red? – PLoS Biol. 2: e350.

Rosas-Guerrero, V. et al. 2014. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? – Ecol. Lett. 17: 388–400.

Schmid, B. et al. 2016. Responses of nectar-feeding birds to floral resources at multiple spatial scales. – Ecography. 39: 619–629.

Schmid, S. et al. 2011. Diversity of flower visitors and their role for pollination in the ornithophilous bromeliad *Vriesea friburgensis* in two different habitats in southern Brazil. – Ecotropica 17: 91–102.

Stebbins, G. L. 1970. Adaptive variation of reproductive characteristics in Angiosperms, I: pollination mechanisms. – Annu. Rev. Ecol. Syst. 1: 307–326.

Stiles, F. 1981. Geographical aspects of bird-flower coevolution, with particular reference to Central America. – Ann. Miss. Bot. Gard. 68: 323–351.

Stiles, F. G. 1985. Seasonal patterns and coevolution in the hummingbird-flower community of a Costa Rican subtropical forest. – Ornithol. Monogr. 36: 757–787.

Strauss, S. Y. et al. 2004. Optimal defence theory and flower petal colour predict variation in the secondary chemistry of wild radish. – J. Ecol. 92: 132–141.

Stromberg, M. R. and Johnsen, P. B. 1990. Hummingbird sweetness preferences: taste or viscosity? – Condor 92: 606.

Thomson, J. D. et al. 2000. Pollen presentation and pollination syndromes, with special reference to Penstemon. – Plant Species Biol. 15: 11–29.

Tripp, E. A. and McDade L. A. 2013. Time-calibrated phylogenies of hummingbirds and hummingbird-pollinated plants reject a hypothesis of diffuse co-evolution. – Aliso 31: 89–103.

Urcelay, C. et al. 2006. Relationship between corolla length and floral larceny in the South American hummingbird-pollinated *Campsidium valdivianum* (Bignoniaceae). – Ann. Bot. Fenn. 43: 205–211.

Vlašánková, A. et al. 2017. The nectar spur is not only a simple specialization for long-proboscid pollinators. – New Phytol. 215: 1574–1581.

Wang, X. et al. 2020. Plants are visited by more pollinator species than pollination syndromes predicted in an oceanic island community. – Sci. Rep. 10: 13918.

Waser, N. 1983. The adaptive nature of floral traits: ideas and evidence. – In: Real, L. (ed.), Pollination biology, 1st edn. – Academic Press, pp. 213–239.

Waser, N. M. et al. 1996. Generalization in pollination systems, and why it matters. - Ecology 77: 1043–1060.

Wasserthal, L. T. 1997. The pollinators of the Malagasy star orchids Angraecum *sesquipedale*, *A. sororium* and *A. compactum* and the evolution of extremely long spurs by pollinator shift. – Bot. Acta 110: 343–359.

Weinstein, B. G. 2015. MotionMeerkat: integrating motion video detection and ecological monitoring. – Methods Ecol. Evol. 6: 357–362.

Whittall, J. B. and Hodges, S. A. 2007. Pollinator shifts drive increasingly long nectar spurs in columbine flowers. – Nature 447: U706–U712.

Wilson, P. et al. 2004. A multivariate search for pollination syndromes among penstemons. – Oikos 104: 345–361.

Wolf, L. L. and Hainsworth, F. R. 1983. Economics of foraging strategies in sunbirds and hummingbirds. – In: Aspey, W. and Lustick, S. I. (eds), Behavioral energetics: the cost of survival in vertebrates. – Ohio State Univ. Press, pp. 223–264.

Wolff, D. et al. 2003. Nocturnal versus diurnal pollination success in *Isertia laevis* (Rubiaceae): a sphingophilous plant visited by hummingbirds. – Plant Biol. 5: 71–78.

Zanata, T. B. et al. 2017. Global patterns of interaction specialization in bird-flower networks. – J. Biogeogr., 44: 1891–1910.

Zhang, Y. 2013. Likelihood-based and Bayesian methods for tweedie compound poisson linear mixed models. – Stat. Comput. 23: 743–757.

SUPPORTING INFORMATION CHAPTER IV

Chmel, K., Ewome, F.L., **Uceda Gómez, G.**, Klomberg, Y., Mertens, J.E.J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome works as the plant's adaptation to ornithophily, while nectarivorous birds do not seem to care. *Oikos*, 130, 1411-1424. https://doi.org/10.1111/oik.08052

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PART-III SPATIOTEMPORAL VARIABILITY IN SUNBIRD-PLANT INTERACTIONS

Cyanomitra olivacea

Chapter V

Janeček, Š., **Uceda-Gómez, G.**, Janečková, P., Tropek, R., Fominka, N.T., Njie, M.M., Mlíkovský, J., Kamga, S.M., Molua, L.L., & Ewome, F.L. (2024). Food resource partitioning between males and females of Volcano Sunbird *Cinnyris preussi* on Mount Cameroon. *Journal of Ornithology*. https://doi.org/10.1007/s10336-024-02187-8

Chapter VI

Janeček, Š., Chmel, K., Mlíkovský, J., **Uceda-Gomez, G.**, Janečková, P., Fominka, N.T., Njie, M.M., & Ewome, F.L. (2022). Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. *Oecologia*, 199, 885-896. https://doi.org/10.1007/s00442-022-05234-4

Chapter VII

Uceda-Gomez, G., Molua, L.L., Mani, F.T., Ewome, F.L., & Janeček, Š. (manuscript under review; Journal of Plant Ecology) Coping with altitude: Altitude-driven visitor shifts to *Hypericum revolutum* (Hypericaceae) on Mount Cameroon grasslands.

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ORIGINAL ARTICLE

Food resource partitioning between males and females of Volcano Sunbird (*Cinnyris preussi*) on Mount Cameroon

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Abstract

Competition for nectar is expected to result in feeding niche differentiation. Here, we targeted the sexually size-dimorphic Volcano Sunbird (*Cinnyris preussi*) on Mount Cameroon. We investigated whether males and females feed on different plant species, whether females with shorter bills than males prefer shorter flowers, and whether larger dominant males visit more energetic flowers that produce higher amounts of nectar sugars. We also asked whether feeding niches were spatially separated along the elevation gradient and whether this separation varied between the two contrasting seasons. We collected data on the frequency of visits to individual plant species and analyzed the male-to-female ratios in the mist-netted dataset. In addition, we estimated production of nectar sugar in individual habitats and seasons. Despite the large dataset collected, encompassing 6476 bird–plant interactions, our findings did not provide evidence of differences in the spectra of the visited plant species. In addition, females did not visit flowers with shorter tubes, nor did males visit flowers that produced higher amounts of sugars. However, we observed a sex-specific dispersion of sunbirds during the wet season. During the dry breeding season, both males and females feed mainly in nectar-rich montane and submontane forests. In the wet season, the production of nectar sugar in these habitats decreased dramatically, and females largely disappeared. In contrast, female activity increased in the lowest and highest parts of the altitudinal range. Our findings on elevational movements are important in the current context, in which species face potential threats from habitat destruction and climate change.

Keywords Cameroon · *Cinnyris preussi* · Competition · Niche differentiation · Sunbird

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Zusammenfassung

Aufteilung von Nahrungsressourcen zwischen Männchen und Weibchen eines Nektarvogels (*Cinnyris preussi*) auf dem Kamerunberg.

Es wird erwartet, dass die Konkurrenz um Nektar zu einer Differenzierung in der Nahrungsnische führt. Wir untersuchten hier einen Nektarvogelart (Cinnyris preussi) auf dem Kamerunberg, die einen Geschlechtsdimorphismus aufweist. Wir prüften, (1) ob Männchen und Weibchen sich von verschiedenen Pflanzenarten ernähren, (2) ob Weibchen, die einen kürzeren Schnabel als Männchen haben, Blüten mit kürzeren Blütenkelchen bevorzugen und (3) ob die größeren und dominanten Männchen energiereichere Blüten aufsuchen, die größere Mengen an Nektarzucker produzieren. Wir wollten auch wissen, ob die Nahrungsnischen entlang des Höhengradienten räumlich getrennt sind und ob diese räumliche Trennung zwischen den beiden gegenteiligen Jahreszeiten variiert. Wir sammelten Daten über die Besuchshäufigkeit an einzelnen Pflanzenarten und analysierten das Männchen-Weibchen-Verhältnis von in den Japannetzen gefangenen Individuen. Darüber hinaus schätzten wir die Produktion von Nektarzucker in den verschiedenen Lebensräumen und Jahreszeiten. Trotz des großen Datensatzes, der 6.476 Vogel-Pflanzen-Interaktionen umfasste, erbrachten unsere Ergebnisse keine Hinweise auf Unterschiede im Spektrum der aufgesuchten Pflanzenarten. Darüber hinaus besuchten weder die Weibchen gezielt Blumen mit kürzeren Blütenkelchen auf, noch besuchten Männchen Blüten, welche die größeren Mengen an Zucker produzierten. Jedoch beobachteten wir eine geschlechtsspezifische Verteilung der Nektarvögel während der Regenzeit. Während der trockenen Brutzeit gingen sowohl die Männchen als auch die Weibchen vor allem in nektarreichen montanen und submontanen Wäldern auf Nahrungssuche. In der Regenzeit ging die Produktion von Nektarzucker in diesen Lebensräumen drastisch zurück, und die Weibchen verschwanden größtenteils. Im Gegenzug dazu nahm die Aktivität der Weibchen in den niedrigsten und höchsten Teilen des Höhengebiets zu. Unsere Ergebnisse zu den Höhenbewegungen sind wichtig im aktuellen Kontext, in dem Arten durch Zerstörung ihrer Lebensräume und Klimawandel bedroht sind.

Introduction

Competition among nectar-feeding birds is a well-known phenomenon. It can have a character of either simultaneous exploitation of nectar from the same flowers or of a direct interference for resources among individuals (Ford 1979). Regardless of its nature, competition incurs associated costs, and nectarivorous birds tend to mitigate it through niche differentiation (Gill 1978; Janeček et al. 2012). This can be achieved by niche segregation in space, time, or feeding on different co-flowering plant species. Spatial segregation can occur at different scales. Birds can feed on different parts of the same plant (Stiles and Wolf 1970; Ford and Paton 1982; Lara et al. 2009), separate their feeding territories in the same habitat (Lara et al. 2009), use different habitats in relatively small areas (Ford and Paton 1976; Ortiz-Pulido et al. 2012), or migrate to distant, less competitive environments (Bertin 1980; McKinney et al. 2012). Similarly, temporal segregation can occur over short periods, for instance birds can visit the same plants in a given area at different times of the day (Lara et al. 2009) or in different seasons (Araújo and Sazima 2003; Araújo et al. 2013). Differences in the spectra of visited plant species are often related to trait matching between bill and floral morphologies (Kodric-Brown et al. 1984; Janeček et al. 2012; Maglianesi et al. 2014; Weinstein and Graham 2017; Sonne et al. 2019). The competition and need for niche differentiation are not the same throughout the year, but can intensify in times of nectar food shortage (Yeaton and Laughrin 1976; Tinoco et al. 2017). During nectar-poor periods, some habitats can become profitable only for some bird species, whereas other birds need to move to more profitable areas (Wolf 1970; Ford 1979; Collins 1985).

Moreover, feeding niche differentiation can be a consequence of both interspecific and intraspecific competitive interactions, with sexual differentiation serving as a special example of the latter. On a small spatial scale, niche differentiation between the sexes is often related to territorial behavior. Colwell and King (unpublished, cited in Feinsinger and Colwell 1978) observed that males of Green-backed Firecrown (*Sephanoides sephaniodes*) were strongly territorial, whereas females were low-reward trapliners or generalists. Similarly, male Olive Sunbirds (*Cyanomitra olivacea*) defend nectar-rich sources (Frost and Frost 1981). Nevertheless, not only males but also females of hummingbirds (Wolf 1969) or sunbirds (Gill and Wolf 1975) can be territorial.

Sex-specific migration of nectarivorous birds is known to occur in hummingbirds. The males of Broad-tailed Hummingbirds (*Selasphorus platycercus*) disappear from the breeding locality when the feeding conditions become unfavorable, while females stay to take care of the young (Wagner 1945). In addition, sex-specific migrations of the Mexican Violetear (*Colibri thalassinus*) have been reported. While adult females, young males, and some adult males migrate, other adult males stay during the winter in the neighborhood of the breeding range, feeding on remnants of flowering plants (Wagner 1945). In Mato Grosso do Sul, Brazil, males of Black-throated Mango (*Anthracothorax nigricollis*) were observed feeding on plants for only one month, whereas females were also recorded in other periods (Barbosa-Filho and Araujo 2013). In addition, males of Allen's Hummingbird (*Selasphorus sasin*) precede the migration of females from breeding sites (Phillips 1975). Although various movements of other specialized nectarivores are known (e.g., Keast 1968; Craig and Hulley 1994), to the best of our knowledge, information on possible sex differences is missing.

When both sexes occupy the same space, the segregation of feeding niches can be based on differences in their food plant spectra. This segregation is often associated with sexual size dimorphism in birds (Temeles et al. 2010; Berns and Adams 2013; Maglianesi et al. 2022). Sexual size dimorphism has been observed in many phylogenetic lineages of nectarivorous birds. In the Old World, it is relatively rare in honeyeaters (Clarke and Clarke 1999) but common in sunbirds (Cheke et al. 2001). In the New World, sexual size dimorphism is widespread among hummingbirds (Berns and Adams 2013). Males are larger than females in larger-bodied hummingbird species, whereas the opposite is true for smaller species (Colwell 2000; Avalos et al. 2022). It was shown that the long-billed females of Purple-throated Carib (*Eulampis jugularis*) have significantly shorter handling times on deep flowers of the green morph of *Heliconia bihai* than the short-billed males (Temeles et al. 2009). Similarly, the long-billed females of Mountain Velvetbreast (*Lafresnaya lafresnayi*) feed on a different spectrum of plants than males (Snow and Snow 1980), and the females of Fork-tailed Woodnymph (*Thalurania furcata*) feed on floral resources, which exhibit more similarity to another hummingbird species Planalto Hermit (*Phaethornis pretrei*) than *T. furcata* males (Faria and Araújo 2010). Feeding on different plants can also be related to different energy needs, which are a consequence of dimorphism in body size (Brown et al. 1978) or behavior (Riegert et al. 2011).

In our study, we targeted the niche differentiation of the sexually size-dimorphic Volcano Sunbird (*Cinnyris preussi*) on Mount Cameroon. We explored its feeding behavior, spatial distribution, and changes in these characteristics in two contrasting seasons (wet and dry). Our study was performed in five vegetation types along an elevational gradient, and we also investigated the differences in nectar production. We tested several hypotheses and related predictions that originated mainly from hummingbird studies: (1) The sexes of nectarivorous birds can segregate their feeding niches to reduce intraspecific competition. This can be achieved by feeding in the same area on different plants or by spatial movement and feeding in different areas. We expected *C. preussi* females and males to forage on different plant species. During the breeding (dry) season, we anticipate that both sexes will occupy the same geographical area; however, in the non-breeding (wet) season, they will exhibit varying altitudinal distribution patterns. (2) The distinction in niches becomes particularly pronounced during periods of limited food availability. We expected lower nectar sugar production and, consequently, higher niche segregation during the wet season. (3) Plant–pollinator interactions are shaped by mutual trait matching. We expected that *C. preussi* males with longer bills would be more likely to visit long tubular flowers. (4) Body mass is positively related to energy demand and social dominance. We expect that larger males will be dominant over females and, in consequence, will chase the females from the plants; in the case of movement, the females will move to areas with a lower amount of resources. Finally, we expected heavier and socially dominant *C. preussi* males to visit flowers with higher sugar production.

Methods

Study site

Mt. Cameroon is the highest mountain in West and Central Africa and is a global biodiversity hotspot (Myers et al. 2000; Küper et al. 2004; Hoffman et al. 2016). A diverse range of tropical forests can be observed on the slopes of Mt. Cameroon. Despite the extensive destruction and transformation of lowland littoral forests on the southwestern foothills into plantations, pristine forests can be encountered at elevations of approximately 400 m above the sea level. In some areas, these forests have experienced natural disturbances due to the presence of local African Forest Elephant (*Loxodonta cyclotis*) populations (Maicher et al. 2020a). The timberline location varies at different sites, typically falling within the range of 1900–2500 m above sea level. Above the timberline, a wide spectrum of herbaceous communities can be observed ascending to the summit, which is approximately 4040 m above sea level (electronic supplementary material Fig. S1 and Fig. S2). Mt. Cameroon experiences conspicuous seasonality. During the wet season, monthly precipitation locally exceeds 2000 mm, whereas almost no rain occurs during the dry season (Maicher et al. 2020b).

We performed our study at five locations along the altitudinal gradient (electronic supplementary material Fig. S2 and Table S1): (1) the mid-elevational forest (MEF) around the PlanteCam Camp (1100 m a. s. l.), which is partially disturbed by elephants; (2) the submontane forest mosaic (SF) around the Crater Lake locality (1500 m a.s.l.), which is characterized by large elephant pastures and patches of forest; (3) the montane forest (MF) around Mann's Spring (2100 m a. s. l.), near the timberline; (4) the low-elevational montane grasslands (LG) above the timberline near Hut 1 on the Guinness Trail (2100 m a. s. l.), and (5) the high-elevational montane grasslands (HG) near Hut 2 (2800 m a. s. l.). Sampling was performed for approximately 8 weeks at each elevation. Four weeks during the wet season and 4 weeks during the dry season.

Studied species

Volcano Sunbird (Reichenow 1892, Fig. S1) inhabits the highlands of Cameroon, Equatorial Guinea (Bioko) and Nigeria. This taxon was often classified as a subspecies of the Northern Double-collared Sunbird (*C. reichenowi*) (Cheke et al. 2001) under which name it has appeared in the vast majority of sunbird–plant interaction studies (e.g., Janečková et al. 2021; Sejfová et al. 2021; and other cited studies). Nevertheless, it was recently shown to be distinct from that of East African species (Cooper et al. 2021).

C. preussi has, similar to other double-collared sunbirds, pronounced sexual dimorphism. Females are inconspicuously colored, while males display conspicuous coloring. Females are smaller (*t*-test, *t*-value = 11.12, $p < 0.0001$; average female mass: 8.23 ± 0.06 g (SE), $n = 167$; average male mass: 9.14 ± 0.05 g (SE), $n = 261$, our unpublished data; electronic supplementary material Fig. S3) with shorter culmen length, that is the distance from the base of the feather on the culmen to the tip measured as a straight line (*t*-test, *t*-value = 7.89, $p < 0.001$; average female culmen length: 16.40 ± 0.13 mm (SE), $n = 65$; average male culmen length: 17.77 ± 0.10 mm (SE), $n = 140$; data from Cooper et al. 2021; electronic supplementary material Fig. S3).

C. preussii feeds on insects and on nectar (Cheke et al. 2001; Riegert et al. 2011). *C. preussii* visits flowers with a broad spectrum of floral morphologies. It drinks not only from open, morphologically generalized, but also from tubular, morphologically specialized flowers (Janeček et al. 2007, 2011, 2012, 2022). The females lay eggs during the transition from the wet to dry season and the dry season (Serle 1951; Cheke et al. 2001, our personal observations).

Plant trait data collection

To examine the degree of trait matching between *C. preussi* and the flowers they visit, we collected morphological and nectar data of the flowers. We measured tube length using an electronic caliper. We measured at least five randomly selected flowers per species, each from a different plant individual. To estimate nectar sugar production over a 24-h period, we initially marked randomly selected opened flowers on the target plant individual and covered them with mesh bags to prevent nectar consumption by floral visitors. After 24 h, we used these flowers for nectar sampling. Each sample was represented by flowers from one plant individual. We collected at least three samples per species for the rarest plants, but usually at least 15 samples for the common species. To estimate the production of nectar sugar, two nectar-processing methods were used, based on nectar production (1) from flowers with high nectar production, we extracted nectar and measured nectar volume using microcapillary tubes or Hamilton syringes. We measured the nectar concentration using a Pal-1 (Atago Co.) pocket refractometer. (2) When nectar production was too low, we washed the flower with filtered water, transferred it with diluted sugars into an Eppendorf tube, added ethanol, and boiled it for 15 min to deactivate the enzymes (Chlumská et al. 2014). In the laboratory, samples were dried and transferred to constant volumes. The concentrations of individual sugars (i.e., glucose, fructose, and sucrose) were measured by high-performance liquid chromatography using an ICS-3000 system (Dionex) with an electrochemical detector and a CarboPac PA 1 column. The sugar amount (mg) per flower was calculated from both nectar-processing methods. For other information on nectar production see Bartoš et al. (2012) and Janeček et al. (2021) and for floral traits measurements Klomberg et al. (2022). For the analyses, we used the mean tube length and mean nectar sugar production per flower averaged across individual plants within each species.

Transects and estimation of plant community nectar sugar production

To estimate plant abundance and nectar sugar production per unit area, we established six transects for each vegetation type. Each transect was 0.2 ha large, 200 m long, and 10 m wide. In each transect, we counted the number of plants and flowers visited by *C. preussi* during the wet and dry seasons. For nectar sugar production assessment per area, the number of flowers was multiplied by species-specific 24-h nectar sugar production per flower.

Bird observation

The data on plant–*C. preussi* interactions were partly extracted from the larger datasets on plant–nectivorous bird interactions in Mt. Cameroon forest (Janeček et al. 2022) and partly from unpublished datasets from Mt. Cameroon montane grasslands. In this study, only the plants visited by *C. preussi* were considered. We observed birds using timed observations of plant species occurring in or around transects. Compared to transect walking, this method provides sufficient sampling effort for relatively rare and/or rarely visited plants (Gibson et al. 2011), which can nevertheless be a highly specialized bird-pollinated species (Janeček et al. 2015). We designed the observation of plants to be as effective as possible, depending on the environment and plant size. In the tropical forests, we monitored the herbs and smaller shrubs using security cameras (Vivotek IB8367) with a target to record ten individuals of each plant species and each plant individual for two days. Trees and shrubs, which did not fit the camera field view, were observed personally with the target to observe eight individuals of each plant species each for eight hours (for more details, see Janeček et al. 2022). In montane grasslands, where the vegetation is much more open, we observed more plants at one observation point. In grasslands, we also recorded the chasing behavior of males and females. We aimed to observe at least ten individuals of each plant species at different observation points. The average observation time for each plant species was 150 h. Nevertheless, the rarity of some species, together with various logistical and/or technical problems related to the harsh weather on Mt. Cameroon, resulted in different recording times for individual plant species (electronic supplementary material Table S2). Young birds of indeterminate sex, that is, female-like but with a specific behavior and/or bill yellow base, were not considered in this study. Nevertheless, during the study period, the number of these birds was relatively low (4.3% of mist-netted birds were young for which we were not able to determine the sex).

Bird trapping

To support the plant visitation data on *C. preussi* female-to-male ratios in individual vegetation types and seasons, we report bird-trapping data. These data were obtained from two large datasets collected in two projects. The first project was conducted along the forest elevational gradient (partly used by Kamga et al. 2023), whereas the second focused on the grasslands above the timberline. In all locations, we used 16 mm mesh size nets to maximize the chances of catching small passerines such as *C. preussi*. In MEFs and MFs, birds have been caught using ground-to-canopy mist nests (Chmel et al. 2016, 2021; Kamga et al. 2023) and a few ordinary ground nets. At other sites, 10–15 ground nets (12 m each) were used. The nets were operated at the same time for three consecutive days. However, due to the difficulties imposed by the terrain, the length of the nets used varies across locations. When the weather conditions allowed, the nets were opened from 06:00 AM to 06:00 PM.

Statistical analyses

To compare the observed numbers of males and females with the predicted numbers in the ratio of 1:1, we used the chi-square test. The associations between sex and season were tested in 2 × 2 contingency tables using Fisher's exact tests. Statistical analyses were conducted using R software (R Core Team 2023).

Visitation frequencies per hour were calculated first per plant and then per area. To estimate the frequency of visits per area, we used 0.2 ha transects. The frequency of visits per transect (T) was estimated for each transect as:

$$T = \sum_{i=1}^{n} A_i \times F_i,$$

where A_i is the number of individuals of plant species i on the transect and F_i is the mean frequency of visits per one individual of plant species i. The data on visitation frequencies by males and females on individual plants contained many zeros, and consequently, were not normally distributed. Therefore, we tested the effects of the study site, season, bird sex, and their interactions using the nonparametric permutation test in the *PERMANOVA* program, which is an extension of the *PRIMER* software (Anderson et al. 2008). Plant ID was nested as a random factor in study site × season. Visitation frequency data were log $(x+1)$ transformed to decrease the effect of extreme values.

The effects of season and study site on biotope nectar sugar production were tested by repeated-measures ANOVA in the program *Statistica*, with factor season considered as a repeated-measures factor (TIBCO Software Inc. 2020).

We calculated the food niche overlap using a bird sex versus plant species matrix. The cell entries represent the interaction frequencies (i.e., the number of visits per hour). Niche overlap was expressed as Morista's similarity index (Morisita 1959) using the niche overlap function in the R package *spaa* (Zhang 2016). The index ranges from 0 (the sexes do not share any plants) to 1 (they feed with the same frequency on the same resources). We tested the observed overlap with the null modeled overlaps, which were calculated after 1000 randomizations of visitation matrix data. In each randomization we (1) created the *C. preussi* sex vs. plant individuals matrix with the cell entries as the number of visits (2) which were then randomly redistributed with the restrictions that the row and column totals were fixed. In other words, the total number of visits by individual bird sex and the total number of visits to individual plants did not change. (3) The bird sex × plant individuals matrix was recalculated into a bird sex × plant species matrix with cells being the interaction frequencies, and the null model Morista's similarity index was calculated.

We tested the relationship between the proportion of female visits on individual plant species (dependent variable) and their mean tube length and nectar sugar production per flower using linear regressions in the Statistica program (TIBCO Software Inc. 2020). Although proportions, the data distribution on female visits did not significantly differ from the normal distribution (Kolmogorov–Smirnov test, $d = 0.14$, $p > 0.20$) and consequently we did not use any data transformation.

Results

In total, we recorded 6476 visits by *C. preussi* on 44 plant species (Fig. 1), including 4137 males and 2339 females. The total number of visits by males and females significantly differed from the 1:1 ratio (Chi-square = 499.2, $p < 0.001$). There was also a significant association between bird sex and season (Fisher's exact test, $p < 0.001$). The male-to-female ratio of observed visits was lower in the dry season (1.32:1) and higher in the wet season (3.38:1). The differences between sexes in the number of observed visits were significant in both the dry (Chi-square = 83.27, $p < 0.001$) and wet (Chi-square = 653.76, $p < 0.001$) seasons. The number of visits by males and females also differed from the 1:1 ratio in the individual study sites and seasons, except for the highest elevation in the dry season (Table 1). When significant, more visits by males were always observed, except for the lowest elevation in the MEF during the wet season, with a much higher number of observed females (Fig. 1; Table 1). The season-bird sex associations differed in three of the four tested study sites (Table 1). At all these sites, there was a higher proportion of females observed during the dry season. No *C. preussi* individuals were observed in the MEF during the dry season; consequently, this test was not performed. The study site, season, bird sex, and their interactions significantly influenced the frequency of visits, regardless of whether they were calculated per plant or per area (Table 2). The visitation frequency patterns of males and females were similar in the dry season, but differed in the wet season. In the dry season, both males and females had the highest visitation frequencies in the MFs and SFs when calculated per plant and area, respectively. In the wet season, the frequency per plant and per area increased in montane grasslands, but decreased in SFs. During the wet season, females had the highest frequencies per plant and per unit area at both the highest and the lowest elevations (Fig. 2).

In total, we mist-netted 513 *C. preussi* individuals: 289 males and 224 females. The total number of mist-netted males and females significantly differed from the 1:1 ratio (Chi-square = 8.24, $p = 0.004$). There was a significant association between sex and season (Fisher's exact test, $p < 0.001$). The male-to-female catching ratio was 0.93:1 in the dry season, and the difference between the number of caught males and females was not significant (Chi-square = 0.37, $p = 0.543$), whereas it was 1.89:1 in the wet season, and the difference was highly significant (Chi-square = 23.15, $p < 0.001$). The male-to-female ratios did not differ from the 1:1 ratio at the individual sites during the dry season (Table 3). In the wet season, there were significantly more males in the HG and MF. The number of males was also higher (but not significantly) at other sites, except for the lowest study site in the MEF (Table 3).

Nectar sugar production at individual study sites along the elevational gradient differed between seasons (repeated-measures ANOVA, Study site: $F = 3.55$, $p = 0.020$; Season: $F = 9.21$, $p = 0.006$, Season*Study site: $F = 3.14$, $p = 0.032$). At all study sites, higher nectar sugar production was recorded in the dry season, and when all study sites were combined, nectar sugar production was eight times higher than that in the wet season. The highest sugar production by plants visited by *C. preussi* was recorded in the MF, followed by the SF, in the dry season (Fig. 3). In this time, the nectar sugar production was driven by flowering trees such as *Astropanax abyssinicum* (Araliaceae), *Nuxia congesta* (Stilbaceae) in MF, or *Tabernaemontana ventricosa* (Apocynaceae) in SF. During the wet season, the highest nectar sugar source was *Psychotria peduncularis* var. *hypsophila* (Rubiaceae) in MFs, and various *Impatiens* spp. (Balsaminaceae), *Anthocleista scandens* (Gentianaceae) or *Clerodendrum silvanum* (Lamiaceae) in the lower elevations. In both montane grassland sites, nectar sugar production was driven by *Hypericum revolutum* (Hypericaceae) in the dry season and by *Phyllopentas schimperi* (Rubiaceae), and partly by *H. revolutum* in the wet season.

We did not find any evidence of male versus female niche segregation in the spectrum of the visited plant species because the observed niche overlaps did not differ from the overlaps generated by the null models (Table 4). This was true not only for individual site-season combinations but also for specific models for individual seasons and the entire model, including visitation frequencies for all studied plants.

When comparing the traits of plants visited by *C. preussi* and the proportion of visits by females, we did not find any significant effect of nectar sugar production ($r = -0.0293$, $p = 0.854$) or tube length ($r = 0.14$, $p = 0.357$). Similarly, insignificant differences were observed in separate analyses for the dry (nectar sugar production: $r = -0.03$, $p = 0.873$; tube length $r = 0.13$; $p = 0.526$) and wet (nectar sugar production: $r = -0.08$, $p = 0.698$; tube length $r = 0.33$, $p = 0.100$) seasons. In addition, the unimodal distribution of floral lengths of the visited plant species did not indicate niche partitioning (electronic supplementary material Fig. S4).

On montane grasslands, where we have been recording chasing behavior, we observed a significantly higher number of attacks by males than by females (males: $n = 63$, females: $n = 1$; chi-square = 60.06, $p < 0.001$). Males attacked other males more often ($n = 39$) than females ($n = 24$). Nevertheless, this difference was only marginally significant (chi-square = 3.57, $p = 0.059$). The only recorded attack by a female was on another female. No attacks by females on males were recorded.

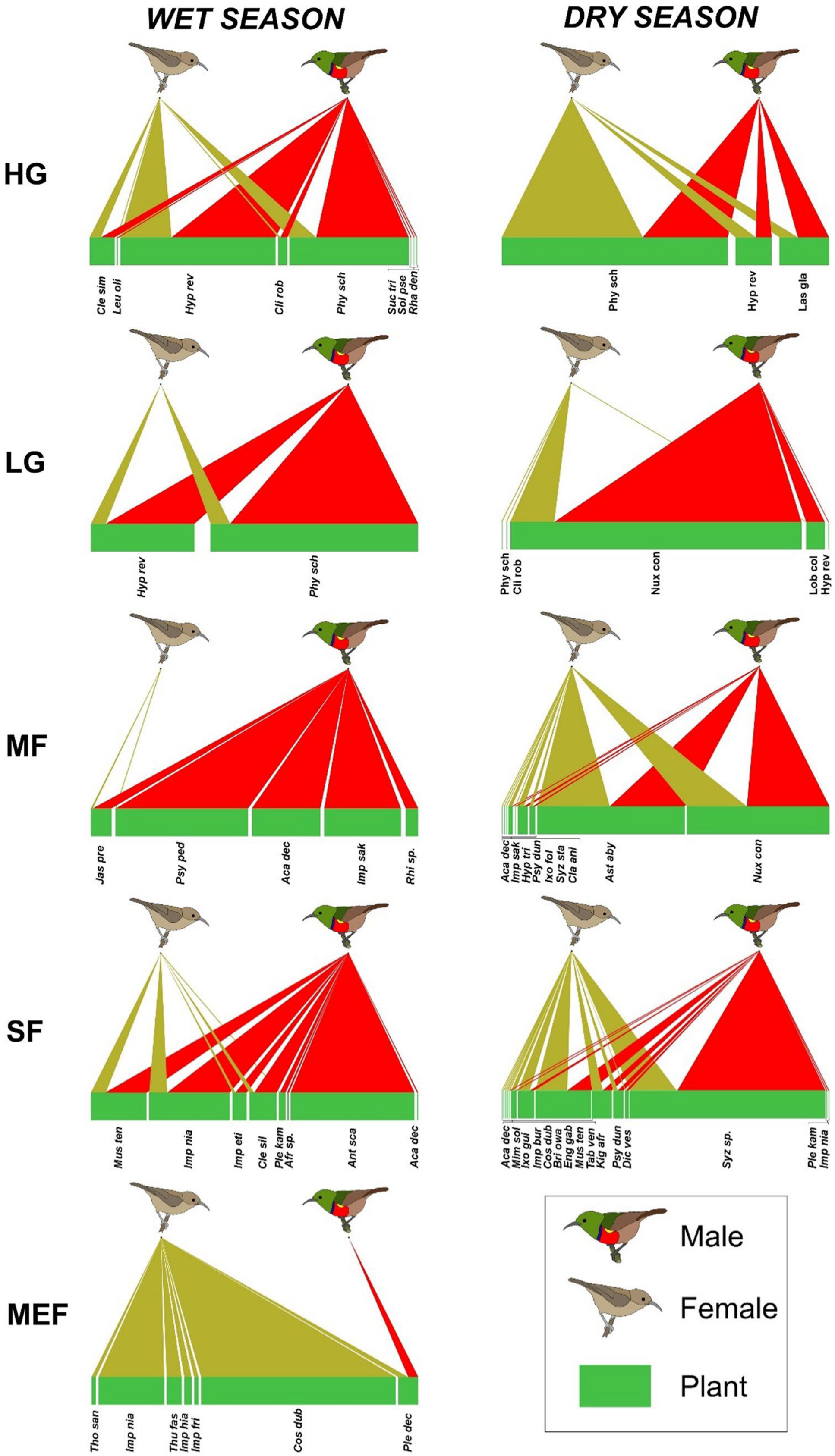

Fig. 1 Feeding of *C. preussi* males and females on flowering plants in different vegetation types and seasons. The sizes of the bars, which represent the plant species, are proportional to the visitation frequency per plant. VEGETATION TYPES: MEF—mid-elevation forest; SF—submontane forest; MF—montane forest; LG—the low-elevational montane grasslands; HG—the high-elevational montane grasslands. PLANTS: *Aca dec*—*Acanthopale decempedalis*; *Afr* sp.—*Aframomum* sp.; *Ant sca*—*Anthocleista scandens*; *Ast aby*—*Astropanax abyssinicum*; *Bri owa*—*Brillantaisia owariensis*; *Cla ani*—*Clausena anisata*; *Cle sim*—*Clematis simensis*; *Cle sil*—*Clerodendrum silvanum*; *Cli rob*—*Clinopodium robustum*; *Cos dub*—*Costus dubius*; *Dic ves*—*Dicranolepis vestita*; *Eng gab*—*Englerina gabonensis*; *Hyp rev*—*Hypericum revolutum*; *Hyp tri*—*Hypoestes triflora*; *Imp bur*—*Impatiens burtonii*; *Imp eti*—*Impatiens etindensis*; *Imp fri*—*Impatiens frithii; Imp hia*—*Impatiens hians*; *Imp nia*—*Impatiens niamniamensis*; *Imp sak*—*Impatiens sakeriana*; *Ixo fol*—*Ixora foliosa*; *Ixo gui*—*Ixora guineensis*; *Jas pre*—*Jasminum preussii*; *Kig afr*—*Kigelia africana*; *Las gla*—*Lasiosiphon glaucus*; *Leu oli*—*Leucas oligocephala*; *Lob col*—*Lobelia columnaris*; *Mim sol*—*Mimulopsis solmsii*; *Mus ten*—*Mussaenda tenuiflora*; *Nux con*—*Nuxia congesta*; *Phy sch*—*Phyllopentas schimperi*; *Ple dec*—*Plectranthus decurrens*; *Ple kam*—*Plectranthus kamerunensis*; *Psy ped*—*Psychotria peduncularis var. hypsophila*; *Psy dun*—*Psydrax dunlapii*; *Rha den*—*Rhabdotosperma densifolia*; *Rhi* sp.—*Rhipidoglossum* sp.; *Sol pse*—*Solanum pseudospinosum*; *Suc tri*—*Succisa trichotocephala*; *Syz sta*—*Syzygium staudtii*; *Syz* sp.—*Syzygium* sp.; *Tab ven*—*Tabernaemontana ventricosa*; *Tho san*—*Thonningia sanguinea*; *Thu fas*—*Thunbergia fasciculata*

Table 1 Number of observed visits of males (m) and females (f) to individual study sites

	Dry season				Wet season				Season × sex association
	m	f	Chi-square	p	m	f	Chi-square	p	p
HG	64	87	1.72	0.061ns	973	373	267.46	**< 0.001***	**< 0.001***
LG	203	24	141.15	**< 0.001***	133	15	94.081	**< 0.001***	1.000ns
MF	1553	1389	9.14	**0.002***	337	3	328.11	**< 0.001***	**< 0.001***
SF	611	335	80.52	**< 0.001***	262	52	140.45	**< 0.001***	**< 0.001***
MEF					1	61	58.065	**< 0.001***	

Results of chi-square tests comparing the observed number of visits with the predicted number of visits when the female/male visitation ratio will be 1. In the last column the *p*-value of Fisher's exact test testing association between bird sex and season in individual study sites. To control for the family wise error rate, we considered the Bonferroni adjustment. For individual chi-square tests, only *p*-values < 0.0055 were accepted to be significant. Non-significant *p*-values are indicated by "ns", significant ones are in bold and marked by "*"

HG the high-elevational montane grasslands; *LG* the low-elevational montane grasslands; *MF* the montane forest; *SF* the submontane forest mosaic; *MEF* the mid-elevational forest

Table 2 Permutation analyses of the effects of the study site, season, bird sex, and their interactions on visitation frequency per plant (visits*plant^{-1}*h^{-1}) or per transect (visits*transect^{-1}*h^{-1}) of *C. preussi* (see also related Fig. 1)

	Per plant			Per transect	
	df	F_{ps}	p_{perm}	F_{ps}	p_{perm}
Study site (Ss)	4	14.82	**0.001**	35.64	**0.001**
Season (Se)	1	3.50	**0.049**	15.81	**0.001**
Sex	1	55.68	**0.001**	35.02	**0.001**
Ss*Se	4	17.18	**0.001**	106.35	**0.001**
Ss*Sex	4	8.28	**0.001**	8.07	**0.001**
Se*Sex	1	36.30	**0.001**	44.89	**0.001**
Ss*Se*Sex	4	6.71	**0.001**	10.50	**0.001**

Significant *p*-values are in bold

Discussion

Despite the huge dataset on *C. preussi*–plant interactions that we collected, we did not confirm our expectation that males and females would segregate their feeding niches by visiting different plant spectra when staying at the same locality. The highest number of bird visits by both sexes was recorded in MF and SF during the dry season when the availability of nectar sugar was high. Dominant males have been observed chasing females from plants. In times of food shortage, when *C. preussi* do not breed, females have partly disappeared from the MF and SF, and were much more frequently observed in the upper and lower parts of the altitudinal range.

We suppose that the absence of expected trait matching, evident in the similar spectra of plants visited by males and females as well as the lack of correlation between the proportion of female visits and both floral tube length and nectar sugar production, can be explained by several factors. The most important factor seems to be the high proportion of nectar-rich generalized plants that are frequently visited by sunbirds. This was true mainly in the dry season, when the observed niche overlap was notably high, although not significantly greater than that predicted by the null model. In the MF, during the dry season, trees *Astropanax abyssinicum*, *Nuxia congesta*, and *Syzigium staudtii* were the plants most frequently visited by *C. preussi* (Fig. 1; Janeček et al. 2022). In the SF, during the dry season, the most visited plants were trees *Syzigium* sp. and *Tabernaemontana ventricosa*. The flowers of these trees do not have floral tubes (*A. abyssinicum*, *Syzigium* spp.), or the tubes are relatively short (*N. congesta*); consequently, nectar can be easily accessed by both males and females. *T. ventricosa* has a bit longer floral tube, but it is a plant adapted to moths and in consequence does not fit the morphology of sunbirds' bills. In montane grasslands, one of the most visited plants in both the dry and wet seasons is *Hypericum revolutum*, a bee-pollinated plant with flat, morphologically generalized flowers (Fig. S1a; Janeček et al. 2007; Bartoš et al. 2015). Specialized ornithophilous plants that specialize in bird pollination predominantly flower on Mt. Cameroon during the wet season (Janeček et al. 2011, 2015; Bartoš and Janeček 2014; Klomberg et al. 2022). In addition, Uceda-Gómez et al. (2024) demonstrated on sunbird species level that trait matching is more important during this season. Nevertheless, precise trait matching in the entire sunbird-plant network seems to be obscured by asymmetry in the relationship between ornithophilous plants and sunbirds (Chmel et al. 2021). Sunbirds do not care much and visit many other non-specialized plants in both the wet and dry seasons (Chmel et al. 2021; Janeček et al. 2022). Moreover, the absence

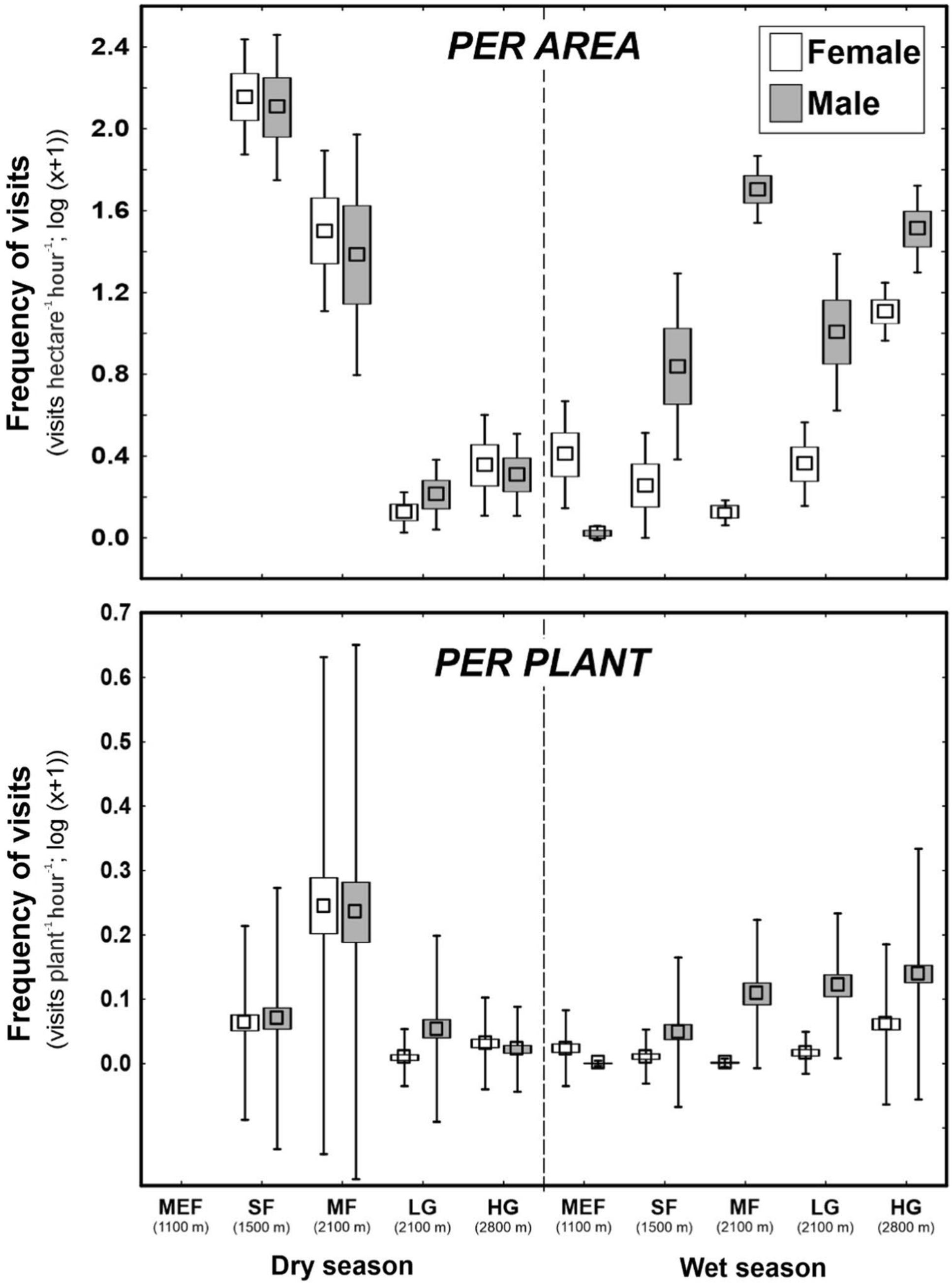

Fig. 2 Visitation frequencies of males and females of *C. preussi* in different study sites and seasons are expressed as the number of visits per area (upper part) or per plant (lower part). HG—the high-elevational montane grasslands; LG—the low-elevational montane grasslands; MF—the montane forest; SF—the submontane forest mosaic; MEF—the mid-elevational forest. Box: mean ± SE; Whisker: mean ± SD

of expected segregation could, to some extent, be caused by the relatively small differences in male and female bill lengths. Although less effective, nectar can be harvested by a protruding tongue and may be taken from flowers deeper than the bill length (Collins 2008). Unfortunately, information on sex specificity or similarity in plant spectra for other sunbird species is absent or fragmentary (e.g., Hobbhahn and Johnson 2015). Our results do not support the results of studies on hummingbirds, which showed that size-dimorphic nectarivorous birds feed on different plant spectra (Taylor and White 2007; Faria and Araújo 2010). Nevertheless, this could also be the result of more pronounced sexual size dimorphism and higher specialization in some hummingbird species (Colwell 2000; Avalos et al. 2022).

In contrast to the differences in floral spectra, our results indicate spatial niche separation. On the small scale, we often observed the chasing of subordinate females by dominant males. This is in agreement with other studies on sunbird territoriality and male dominance (Frost and Frost 1981; Evans and Hatchwell 1992). During other studies in Bamenda Highlands (Cameroon), near our field station we even observed a male of *C. preussi* chasing out his own female from some plants of *Hypoestes aristata* but letting

Table 3 Number of mist-netted males (m) and females (f) at individual study sites

	Dry season				Wet season				Season × sex association
	m	f	Chi-square	*p*	m	f	Chi-square	*p*	*p*
HG	7	4	0.82	0.366^{ns}	71	42	7.44	**0.006***	1.000^{ns}
LG	18	29	2.57	0.109^{ns}	31	27	0.28	0.599^{ns}	0.168^{ns}
MF	60	61	0.01	0.928^{ns}	40	6	25.13	**< 0.001***	**< 0.001***
SF	45	46	0.01	0.917^{ns}	16	6	4.55	0.033^{ns}	0.059^{ns}
MEF					1	3	1.00	0.317^{ns}	

Results of chi-square tests comparing the observed number of visits with the predicted number of visits when the female/male visitation ratio will be 1. In the last column the *p*-value of Fisher's exact test testing association between bird sex and season in individual study sites. To control for the family wise error rate, we considered the Bonferroni adjustment. For individual chi-square tests, only *p*-values < 0.0055 were accepted to be significant. Non-significant *p*-values are indicated by "ns", significant ones are in bold and marked by "*"

HG the high-elevational montane grasslands; *LG* the low-elevational montane grasslands; *MF* the montane forest; *SF* the submontane forest mosaic; *MEF* the mid-elevational forest

her drink on others (see also Padyšáková et al. 2013). In the same locality, *C. preussi* has been observed to protect *H. aristata* from other pollinating species, including carpenter bees (Tropek et al. 2013). Nevertheless, as demonstrated for Rufous Hummingbirds (*Selasphorus rufus*), this space and resource division does not necessarily need to be disadvantageous for females, and they can compensate for it with lower costs and greater success in robbing from rich male territories (Carpenter et al. 1993). Our results are in accordance with previous observations that *C. preussi* individuals move along the altitude during the wet season (Serle 1951; Cheke et al. 2001). Nevertheless, this movement is not only a simple shift from the MF to lower elevations, as expected (Serle 1951; Cheke et al. 2001), but also a more complex and sex-specific dispersion from the MF upward and downwards. However, ringing and/or bird tracking data are required to obtain a more accurate picture of these movements. Unfortunately, the use of both methods is so far not realistic, as the first method is limited by a low ringing effort on Mt. Cameroon, and the second by the absence of sufficiently light tracking devices to be carried by small sunbirds.

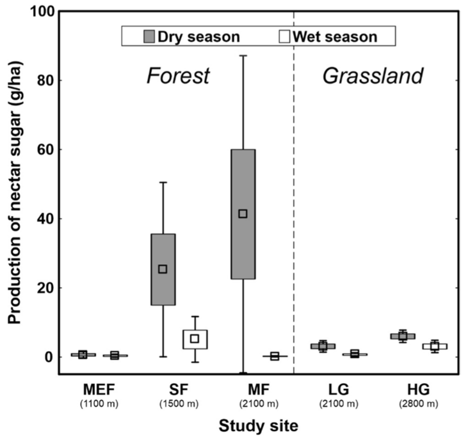

Fig. 3 Production of nectar sugar at individual study sites during the wet and dry seasons. HG—the high-elevational montane grasslands; LG—the low-elevational montane grasslands; MF—the montane forest; SF—the submontane forest mosaic; MEF—the mid-elevational forest. Box: mean ± SE; Whisker: mean ± SD

When comparing the male-to-female ratios in the observation and mist-netting datasets, two common trends were found: (1) a higher proportion of males in the montane and SF in the wet season compared to the dry season and (2) higher proportions of females in lowest elevation during the wet season. The most obvious difference was the much higher proportion of males in the flower visitation dataset than in the mist-netting dataset during the dry season. We assume that this can be caused by higher territoriality in the dry season associated with breeding and/or a high abundance of *C. preussi* in the montane and SFs. Males visit plants not only because they are hungry but also as part of the territory-defending strategy when they aim to keep the levels of nectar in the flowers as low as possible (Paton and Carpenter 1984). Nevertheless, mist netting can also be biased to some extent by the different behaviors of the individual sexes (Borgella et al. 2001).

To gain comprehensive knowledge of male and female movement, it is necessary to explore other slopes and/or habitats. For example, we observed that during wet seasons, both *C. preussi* females and males fed on garden plants in the village of Bokwango (suburban area of Buea, approximately 900 m a. s. l.), but they disappeared in the dry season. Similarly, the limitation of our study is that sampling in each vegetation type and season was performed only once, that is, during one expedition. Consequently, we have not been able to reveal the potential temporal variability across years. Although this study aimed to test more general hypotheses, it also has an important message for conservation. The local

Table 4 Number of recorded visits by females and males

	No. of females	No. of males	Niche overlap observed	Niche overlap null model	*p*-value
Whole model	2339	4137	0.94	0.79	0.177^{ns}
Dry season	1835	2431	0.95	0.80	0.160^{ns}
Wet season	504	1706	0.68	0.74	0.226^{ns}
HG					
Dry	87	64	0.97	0.94	0.371^{ns}
Wet	373	973	0.97	0.93	0.435^{ns}
LG					
Dry	24	203	1.00	0.23	0.032^{ns}
Wet	15	133	1.00	0.88	0.250^{ns}
MF					
Dry	1389	1553	1.00	0.85	0.180^{ns}
Wet	3	337	0.34	0.40	0.429^{ns}
SF					
Dry	335	611	0.80	0.85	0.242^{ns}
Wet	52	262	0.53	0.50	0.354^{ns}
MEF					
Wet	61	1	0.05	0.47	0.272^{ns}

The observed niche overlaps and average null model niche overlaps were calculated using Morista's similarity index. The *p*-value was calculated as the probability that the observed overlap was higher or lower than that predicted by the null model. To control for the family wise error rate, we considered the Bonferroni adjustment. For individual tests of the study site and seasons, only *p*-values <0.0055 were accepted as significant. Non-significant *p*-values are indicated by "ns"

HG the high-elevational montane grasslands; *LG* the low-elevational montane grasslands; *MF* the montane forest; *SF* the submontane forest mosaic; *MEF* the mid-elevational forest

migration of sunbirds is not well known, and only a few anecdotal observations have been reported for some species (Cheke et al. 2001). Nevertheless, these local migrations and movements face several conservation challenges, such as long-distance migrations (Bairlein 2016; Flack et al. 2022). For example, long-distance migrants and locally moving birds are dependent on resources in several habitats. Consequently, these birds can also be, compared to the sedentary species, more threatened by habitat destruction, habitat loss or climatic changes. In the case of nectarivores, climatic changes can influence the synchronization of habitat flowering. Consequently, the presence of nectivorous birds and convenient plant flowering may be mismatched (McKinney et al. 2012). However, nectarivorous birds can find new resources in anthropogenic habitats, such as urban areas, gardens, and flower plantations (Maruyama et al. 2019; Janeček et al. 2020). These threats require further studies to be incorporated into conservation planning.

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Data availability The datasets are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

References

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Araújo AC, Sazima M (2003) The assemblage of flowers visited by hummingbirds in the "capões" of southern Pantanal, Mato Grosso do Sul, Brazil. Flora 198:427–435. https://doi.org/10.1078/0367-2530-00116

Araújo FP, Sazima M, Oliveira PE (2013) The assembly of plants used as nectar sources by hummingbirds in a Cerrado area of Central Brazil. Plant Syst Evol 299:1119–1133. https://doi.org/10.1007/s00606-013-0783-0

Avalos G, Triana F, Klank J (2022) Variation in sexual size dimorphism and fit to Rensch' s rule in 45 species of Costa Rican hummingbirds. Res Square. https://doi.org/10.21203/rs.3.rs-1992118/v1

Bairlein F (2016) Migratory birds under threat. Science 354:547–548. https://doi.org/10.1126/science.aah6647

Barbosa-Filho WG, de Araujo AC (2013) Flowers visited by hummingbirds in an urban Cerrado fragment, Mato Grosso do Sul, Brazil. Biota Neotrop 13:21–27. https://doi.org/10.1590/S1676-06032013000400001

Bartoš M, Janeček Š (2014) Pollinator-induced twisting of flowers sidesteps floral architecture constraints. Curr Biol 24:793–795. https://doi.org/10.1016/j.cub.2014.07.056

Bartoš M, Janeček Š, Padyšáková E, Patáčová E, Altman J, Pešata M, Kantorová J, Tropek R (2012) Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: a comparison with six other co-flowering species. S Afr J Bot 78:63–74. https://doi.org/10.1016/j.sajb.2011.05.015

Bartoš M, Tropek R, Spitzer L, Padyšáková E, Janšta P, Straka J, Tkoč M, Janeček Š (2015) Specializaton of pollination systems of two co-flowering phenotypically generalized *Hypericum* species (Hypericaceae) in Cameroon. Arthropod Plant Interact 9:241–252. https://doi.org/10.1007/s11829-015-9378-8

Berns CM, Adams DC (2013) Becoming different but staying alike: patterns of sexual size and shape dimorphism in bills of hummingbirds. Evol Biol 40:246–260. https://doi.org/10.1007/s11692-012-9206-3

Bertin RI (1980) The Ruby-throated Hummingbird and its major food plants: ranges, flowering phenology, and migration. Can J Zool 60:210–219. https://doi.org/10.1139/z82-029

Borgella R, Snow AA, Gavin TA (2001) Species richness and pollen loads of hummingbirds using forest fragments in southern Costa Rica. Biotropica 33:90–109. https://doi.org/10.1111/j.1744-7429.2001.tb00160.x

Brown JH, Calder WA III, Kodric-Brown A (1978) Correlates and consequences of body size in nectar-feeding birds. Am Zool 18:687–700. https://doi.org/10.1093/icb/18.4.687

Carpenter FL, Hixon MA, Temeles EJ, Russell RW, Paton DC (1993) Exploitative compensation by subordinate age-sex classes of migrant Rufous Hummingbirds. Behav Ecol Sociobiol 33:305–312. https://doi.org/10.1007/BF00172928

Cheke RA, Mann CF, Allen R (2001) Sunbirds: a guide to the sunbirds, flowerpeckers, spiderhunters and sugarbirds of the world. Yale University Press, New Haven

Chlumská Z, Janeček Š, Doležal J (2014) How to preserve plant samples for carbohydrate analysis? Test of suitable methods applicable in remote areas. Folia Geobot 49:1–15. https://doi.org/10.1007/s12224-013-9153-5

Chmel K, Riegert J, Paul L, Novotný V (2016) Vertical stratification of an avian community in New Guinean tropical rainforest. Popul Ecol 58:535–547. https://doi.org/10.1007/s10144-016-0561-2

Chmel K, Kamga SM, Awa T, Ewome FL, Uceda-Gómez G, Hořák D, Mlíkovský J, Molua LL, Riegert J, Janeček Š (2021) Vertical stratification and seasonal changes of the avian community in Mount Cameroon lowland rainforest. Afr J Ecol 59:655–666. https://doi.org/10.1111/aje.12877

Clarke RH, Clarke MF (1999) The social organization of a sexually dimorphic honeyeater: the Crescent Honeyeater *Phylidonyris pyrrhoptera*, at Wilsons Promontory, Victoria. Aust J Ecol 24:644–654. https://doi.org/10.1046/j.1442-9993.1999.00990.x

Collins BG (1985) Energetic of foraging and resource selection by honeyeaters in forest and woodland habitats of Western Australia. N Z J Zool 12:577–587. https://doi.org/10.1080/03014223.1985.10428307

Collins BG (2008) Nectar intake and foraging efficiency: responses of honeyeaters and hummingbirds to variations in floral environments. Auk 125:574–587. https://doi.org/10.1525/auk.2008.07070

Colwell RK (2000) Rensch's rule crosses the line: convergent allometry of sexual size dimorphism in hummingbirds and flower mites. Am Nat 156:495–510. https://doi.org/10.1086/303406

Cooper JC, Maddox JD, McKague K, Bates JM (2021) Multiple lines of evidence indicate ongoing allopatric and parapatric diversification in an Afromontane sunbird (*Cinnyris reichenowi*). Ornithology 138:1–21. https://doi.org/10.1093/ornithology/ukaa081

Craig JFK, Hulley PE (1994) Sunbird movements: a review, with possible models. Ostrich 65:106–110. https://doi.org/10.1080/00306525.1994.9639672

Evans MR, Hatchwell BJ (1992) An experimental study of male adornment in the Scarlet-tufted Malachite Sunbird: I. The role of pectoral tufts in territorial defense. Behav Ecol Sociobiol 29:413–419. https://doi.org/10.1007/BF00170171

Faria RR, Araújo AC (2010) Flowering phenology and pollination of ornithophilous species in two habitats of Serra da Bodoquena, Mato Grosso do Sul, Brazil. An Acad Bras Cienc 82:843–855

Feinsinger P, Colwell RK (1978) Community organization among neotropical nectar-feeding birds. Am Zool 18:779–795. https://doi.org/10.1093/icb/18.4.779

Flack A, Aikens EO, Kölzsch A, Nourani E, Snell KRS, Fiedler W, Linek N, Bauer HG, Thorup K, Partecke J, Wikelski M, Williams HJ (2022) New frontiers in bird migration research. Curr Biol 20:R1187–R1199. https://doi.org/10.1016/j.cub.2022.08.028

Ford HA (1979) Interspecific competition in Australian honeyeaters—depletion of common resources. Aust J Ecol 4:145–164. https://doi.org/10.1111/j.1442-9993.1979.tb01205.x

Ford HA, Paton DC (1976) Resource partitioning and competition in honeyeaters of genus Meliphaga. Aust J Ecol 1:281–287. https://doi.org/10.1111/j.1442-9993.1976.tb01118.x

Ford HA, Paton DC (1982) Partitioning of nectar sources in an Australian honeyeater community. Aust J Ecol 7:149–159. https://doi.org/10.1111/j.1442-9993.1982.tb01588.x

Frost SK, Frost PGH (1981) Sunbird pollination of *Strelitzia nicolai*. Oecologia 49:379–384. https://doi.org/10.1007/BF00347603

Gibson RH, Knott B, Eberlein T, Memmott J (2011) Sampling method influences the structure of plant–pollinator networks. Oikos 120:822–831. https://doi.org/10.1111/j.1600-0706.2010.18927.x

Gill FB (1978) Proximate costs of competition for nectar. Am Zool 18:753–768. https://doi.org/10.1093/icb/18.4.753

Gill FB, Wolf LL (1975) Economics of feeding territoriality in the golden-winged sunbird. Ecology 56:333–345. https://doi.org/10.2307/1934964

Hobbhahn N, Johnson SD (2015) Sunbird pollination of the dioecious root parasite *Cytinus sanguineus* (Cytinaceae). S Afr J Bot 99:138–143. https://doi.org/10.1016/j.sajb.2015.04.003

Hoffman M, Koenig K, Bunting G, Costanza J, Williams KJ (2016) Biodiversity hotspots (version 2016.1) (2016.1). Zenodo. https://doi.org/10.5281/zenodo.3261807

Janeček Š, Hrázský Z, Bartoš M, Brom J, Reif J, Hořák D, Bystřická D, Riegert J, Sedláček O, Pešata M (2007) Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa. Afr J Ecol 45:607–613. https://doi.org/10.1111/j.1365-2028.2007.00779.x

Janeček Š, Patáčová E, Bartoš M, Padyšáková E, Spitzer L, Tropek R (2011) Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? Oikos 120:178–183. https://doi.org/10.1111/j.1600-0706.2010.18612.x

Janeček Š, Riegert J, Bartoš M, Hořák D, Reif J, Padyšáková E, Fainová D, Antczak M, Pešata M, Mikeš V, Patáčová E, Altman J, Kantorová J, Hrázský Z, Brom J, Doležal J (2012) Food selection by avian floral visitors: an important aspect of plant–flower interactions in West Africa. Biol J Linn Soc 107:355–367. https://doi.org/10.1111/j.1095-8312.2012.01943.x

Janeček Š, Bartoš M, Njabo KY (2015) Convergent evolution of sunbird pollination systems of *Impatiens* species in tropical Africa and hummingbird systems of the new world. Biol J Linn Soc 115:127–133. https://doi.org/10.1111/bij.12475

Janeček Š, Chmel K, Uceda Gomez G, Janečkova P, Chmelová E, Sejfová Z, Luma Ewome F (2020) Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. Ecol Evol 10:1784–1793. https://doi.org/10.1002/ece3.5942

Janeček Š, Chmel K, Ewome FL, Hrubá K, Klomberg Y, Kobe IN, Kouede RD, Mertens JEJ, Njie MM, Tropek R (2021) Differences in nectar traits between ornithophilous and entomophilous plants on Mount Cameroon. Plants 10:1161. https://doi.org/10.3390/plants10061161

Janeček Š, Chmel K, Mlíkovský J, Uceda-Gómez G, Janečková P, Fominka NT, Njie MM, Ewome FL (2022) Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. Oecologia 199:885–896. https://doi.org/10.1007/s00442-022-05234-4

Janečková P, Sejfová Z, Janeček Š, Chmel K, Chmelová E, Ewome FL (2021) Behavioural correlates of drinking speed in two West African sunbird species. Bird Stud 67:540–542. https://doi.org/10.1080/00063657.2021.1917510

Kamga SM, Tamungang SA, Awa T II, Chmel K, Luma Ewome F, Lyonga Molua L, Uceda-Gómez G, Janeček Š, Mlíkovský J, Riegert J (2023) Changes in bird community structure on Mount Cameroon driven by elevational and vertical gradients. Diversity 15:727. https://doi.org/10.3390/d15060727

Keast A (1968) Seasonal movements in the Australian honeyeaters (Meliphagidae) and their ecological significance. Emu 67:159–209. https://doi.org/10.1071/MU967159

Klomberg Y, Tropek R, Mertens JEJ, Kobe IN, Hodeček J, Raška J, Fominka NT, Souto-Vilarós D, Janečková P, Janeček Š (2022) Spatiotemporal variation in the role of floral traits in shaping tropical plant–pollinator interactions. Ecol Lett 25:839–850. https://doi.org/10.1111/ele.13958

Kodric-Brown A, Brown JH, Byers GS, Gori DF (1984) Organization of a tropical island community of hummingbird and flowers. Ecology 65:1358–1368. https://doi.org/10.2307/1939116

Küper W, Sommer JH, Lovett JC, Beentje HJ, van Rompaey RSAR, Chatelain C, Sosef M, Barthlott W (2004) Africa's hotspots of biodiversity redefined. Ann Mo Bot Gard 91:525–535

Lara C, Lumbreras K, González M (2009) Niche partitioning among hummingbirds foraging on *Penstemon roseus* (Plantaginaceae) in central Mexico. Ornitol Neotrop 20:73–83

Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M (2014) Morphological traits determine specialization and resource use in plant-hummingbird networks in the tropics. Ecology 95:3325–3334. https://doi.org/10.1890/13-2261.1

Maglianesi MA, Maruyama PK, Temeles EJ, Schleuning M, Zanata TB, Sazima M, Gutiérrez-Zamora A, Marín-Gómez OH, Rosero-Lasprilla L, Ramírez-Burbano MB, Ruffini AE, Salamanca-Reyes JR, Sazima I, Nuñez-Rosas LE, Arizmendi MC, Rahbek C, Dalsgaard B (2022) Behavioural and morphological traits influence sex-specific floral resource use by hummingbirds across the Americas. J Anim Ecol 91:2171–2180. https://doi.org/10.1111/1365-2656.13746

Maicher V, Delabye S, Murkwe M, Doležal J, Altman J, Kobe IN, Desmist J, Fokam EB, Pyrcz T, Tropek R (2020a) Effects of disturbances by forest elephants on diversity of trees and insects in tropical rainforests on Mount Cameroon. Sci Rep 10:21618. https://doi.org/10.1038/s41598-020-78659-7

Maicher V, Sáfián S, Murkwe M, Delabye S, Przybyłowicz Ł, Potocký P, Kobe IN, Janeček Š, Mertens JEJ, Fokam EB, Pyrcz T, Doležal J, Altman J, Hořák D, Fiedler K, Tropek R (2020b) Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. J Biogeogr 47:342–354. https://doi.org/10.1111/jbi.13740

Maruyama PK, Bonizário C, Marcon AP, D'Angelo G, da Silva MM, da Silva Neto EN, Oliveira PE, Sazima I, Sazima M, Vizentin-Bugoni J, dos Anjos L, Rui AM, Marçal Júnior O (2019) Plant–hummingbird interaction networks in urban areas: generalization and the importance of trees with specialized flowers as a nectar resource for pollinator conservation. Biol Conserv 230:187–194. https://doi.org/10.1016/j.biocon.2018.12.012

McKinney AM, CaraDonna PJ, Inouye DW, Barr B, Bertelsen CD, Waser NM (2012) Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. Ecology 93:1987–1993. https://doi.org/10.1890/12-0255.1

Morisita M (1959) Measuring of interspecific association and similarity between communities. Mem Fac Sci Kyushu Univ Ser E Biol 3:65–80. https://doi.org/10.18960/seitai.11.6_252_4

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. https://doi.org/10.1038/35002501

Ortiz-Pulido R, Díaz SA, Valle-Díaz OI, Fisher AD (2012) Hummingbirds and the plants they visit in the Tehuacán-Cuicaltán biosphere reserve. Mexico Rev Mex Biodivers 83:152–163. https://doi.org/10.22201/ib.20078706e.2012.1.1139

Padyšáková E, Bartoš M, Tropek R, Janeček Š (2013) Generalization versus specialization in pollination systems: visitors, thieves, and pollinators of *Hypoestes aristata* (Acanthaceae). PLoS One 8:e59299. https://doi.org/10.1371/journal.pone.0059299

Paton DC, Carpenter FL (1984) Peripheral foraging by territorial Rufous hummingbirds: defense by exploitation. Ecology 65:1808–1819. https://doi.org/10.2307/1937777

Phillips AR (1975) The migration of Allen' s and other hummingbirds. Condor 77:196–205. https://doi.org/10.2307/1365790

R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Reichenow A (1892) Zur Vogelfauna Von Kamerun. J Ornithol 40:177–195. https://doi.org/10.1007/BF02208272

Riegert J, Fainová D, Antzak M, Sedláček O, Hořák D, Reif J, Pešata M (2011) Food niche differentiation in two syntopic species: a case study from the Cameroon mountains. J Ornithol 152:819–825. https://doi.org/10.1007/s10336-011-0650-0

Sejfová Z, Mlíkovský J, Ewome FL, Janečková P, Klomberg Y, Njie MM, Janeček Š (2021) Sunbirds' tendency to hover: The roles of energetic rewards, inflorescence architecture and rain. J Avian Biol 52:jav.02818. https://doi.org/10.1111/jav.02818

Serle W (1951) The double-collared sunbird *Cinnyris reichenowi* sharpe. Nigerian Field 16:20–21

Snow DW, Snow BK (1980) Relationship between hummingbirds and flowers in the Andes of Colombia. Bull Br Mus Nat Hist 38:105–139

Sonne J, Zanata TB, González AMM, Torres NLC, Fjeldså J, Colwell RK, Tinoco BA, Rahbek C, Dalsgaard B (2019) The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. Biotropica 51:205–2018. https://doi.org/10.1111/btp.12637

Stiles FG, Wolf LL (1970) Hummingbird territoriality at a tropical flowering tree. Auk 87:467–491. https://doi.org/10.2307/4083791

Taylor J, White SA (2007) Observations of hummingbird feeding behaviour at flowers of *Heliconia beckneri* and *H. tortuosa* in southern Costa Rica. Ornitol Neotrop 18:133–138

Temeles EJ, Koulouris CR, Sander SE, Kress WJ (2009) Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird. Ecology 90:1147–1160. https://doi.org/10.1890/08-0695.1

Temeles EJ, Miller JS, Rifkin JL (2010) Evolution of sexual dimorphism in bill size and shape of Hermit Hummingbirds (Phaethornithinae): a role for ecological causation. Phil Trans R Soc B 365:1053–1063. https://doi.org/10.1098/rstb.2009.0284

TIBCO Software Inc. (2020) Data science workbench, version 14. http://tibco.com

Tinoco BA, Graham CH, Aguliar JM, Schleuning M (2017) Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. Oikos 126:52–60. https://doi.org/10.1111/oik.02998

Tropek R, Bartoš M, Padyšáková E, Janeček Š (2013) Interference competition between sunbirds and carpenter bees for the nectar of *Hypoestes aristata*. Afr Zool 48:392–394. https://doi.org/10.3377/004.048.0222

Uceda-Gómez G, Chmel K, Janečková P, Mlíkovský J, Klomberg Y, Ewome FL, Molua LL, Njie MM, Tropek R, Janeček Š (2024) Drivers of sunbird-plant interactions on Mount Cameroon: between neutrality and niche-based processes. Biotropica 56:136–148. https://doi.org/10.1111/btp.13290

Wagner HO (1945) Notes on the life history of the Mexican Violet-ear. Wilson Bull 57:165–187

Weinstein BG, Graham CH (2017) Persistent bill and corolla matching despite shifting temporal resources in tropical hummingbird-plant interactions. Ecol Lett 20:326–335. https://doi.org/10.1111/ele.12730

Wolf LL (1969) Female territoriality in a tropical hummingbird. Auk 86:490–504. https://doi.org/10.2307/4083410

Wolf LL (1970) The impact of seasonal flowering on the biology of some tropical hummingbirds. Condor 72:1–14

Yeaton RI, Laughrin L (1976) Fall resource division in Santa Cruz Island hummingbirds. Wilson Bull 88:272–279

Zhang J (2016) Package 'spaa'. Version 0.2.2, Species association analysis. Retrieved from https://cran.r-project.org/web/packages/spa/spa.pdf

SUPPORTING INFORMATION CHAPTER V

Janeček, Š., **Uceda-Gómez, G.**, Janečková, P., Tropek, R., Fominka, N.T., Njie, M.M., Mlíkovský, J., Kamga, S.M., Molua, L.L., & Ewome, F.L. (2024). Food resource partitioning between males and females of Volcano Sunbird *Cinnyris preussi* on Mount Cameroon. *Journal of Ornithology.* https://doi.org/10.1007/s10336-024-02187-8

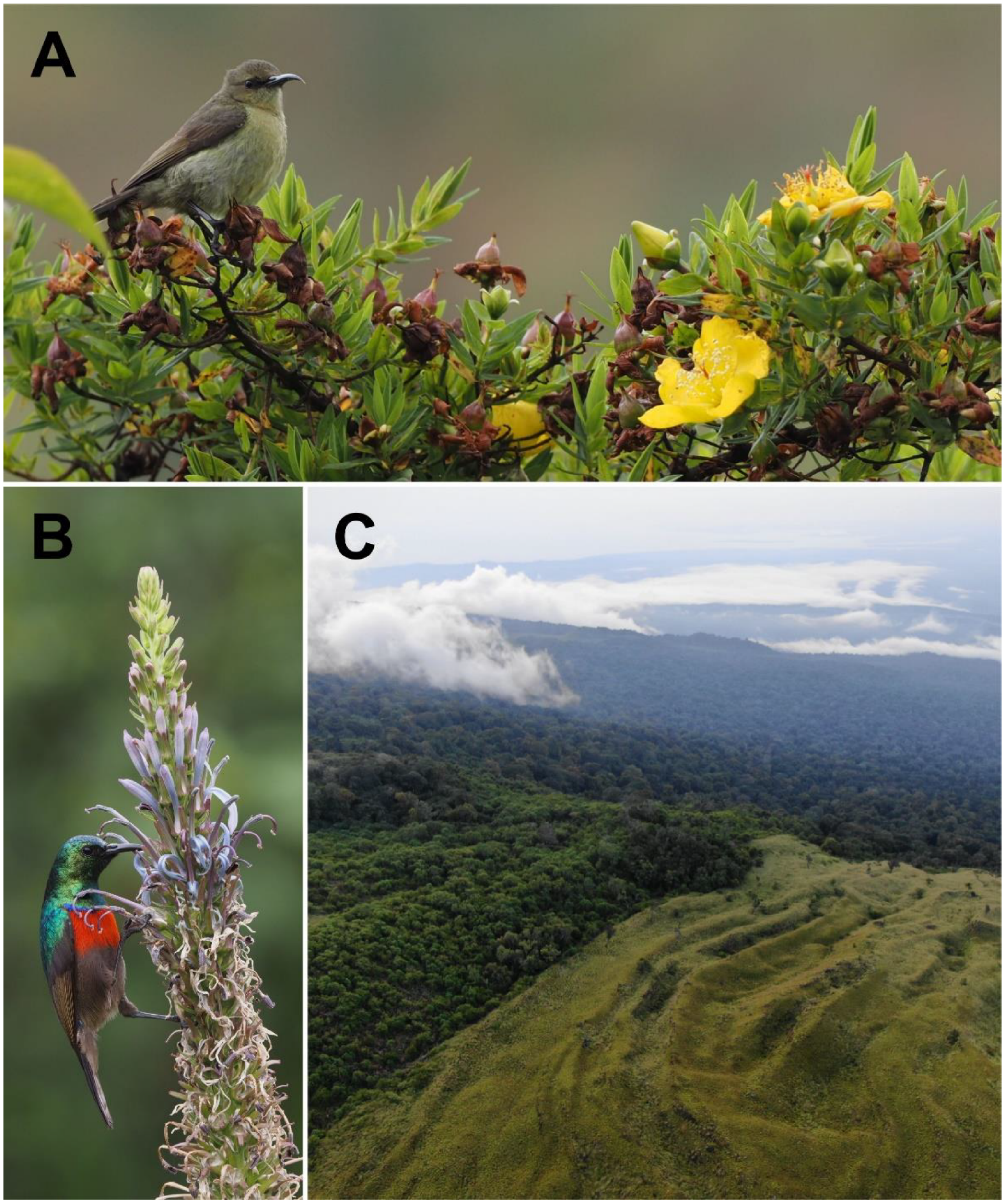

Fig S1. Female of studied species *C. preussi* sitting on *Hypericum revolutum* (**A**). Male *C. preussi* drinking from *Lobelia columnaris* (**B**). Slopes of Mt. Cameroon with an abrupt timberline (**C**).

Supplementary Materials to

Food resource partitioning between males and females of Volcano Sunbird *Cinnyris preussi* on Mount Cameroon

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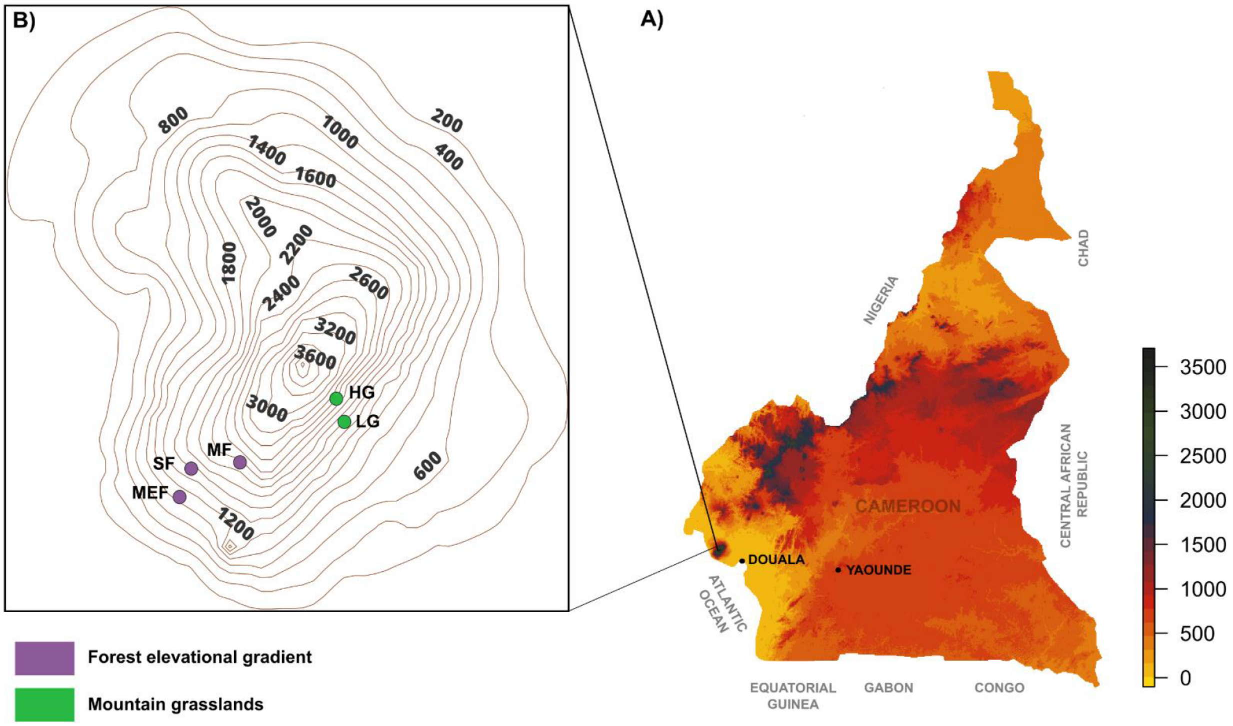

Figure S2. Topographic map of a) Cameroon; b) Mount Cameroon and the sampled locations. In purple locations in the forest elevational gradient: the mid-elevational forest (MEF), the submontane forest mosaic (SF), and the montane forest (MF). In green sampled locations in the montane grasslands: the low-elevational montane grasslands (LG), and the high-elevational montane grasslands (HG).

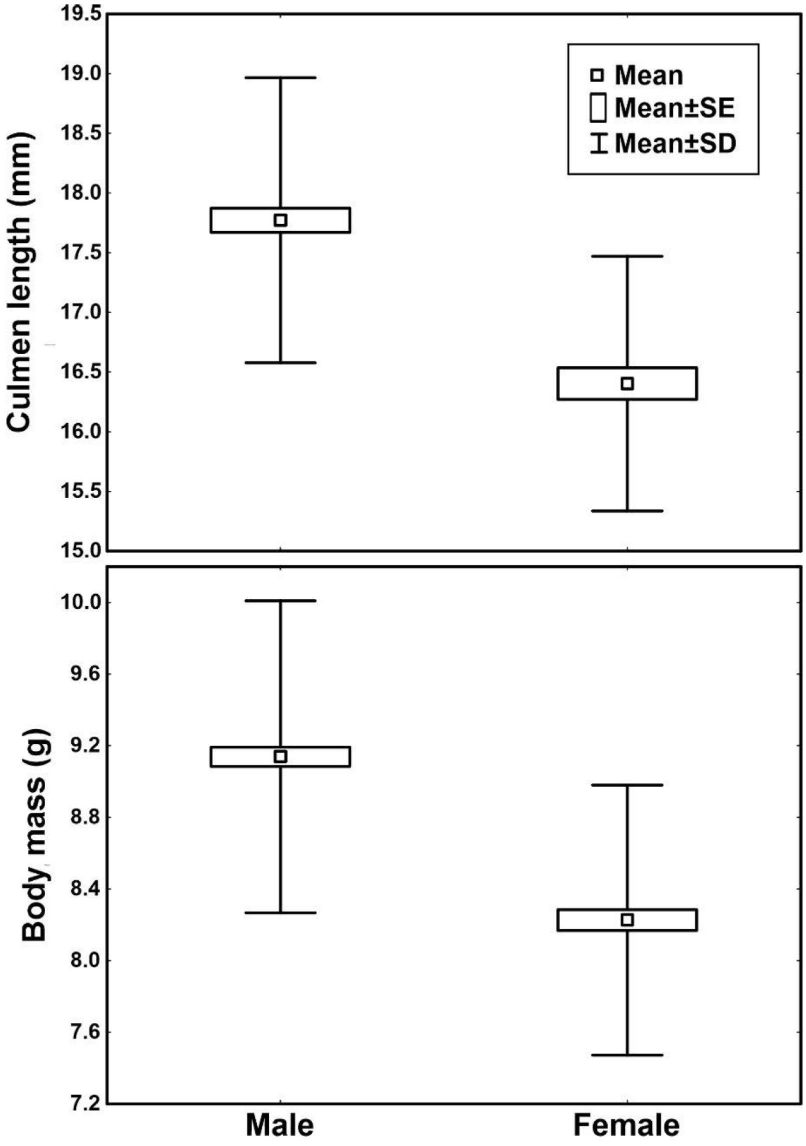

Figure S3. Differences in the body masses and culmen lengths of *Cinnyris preussi* males and females.

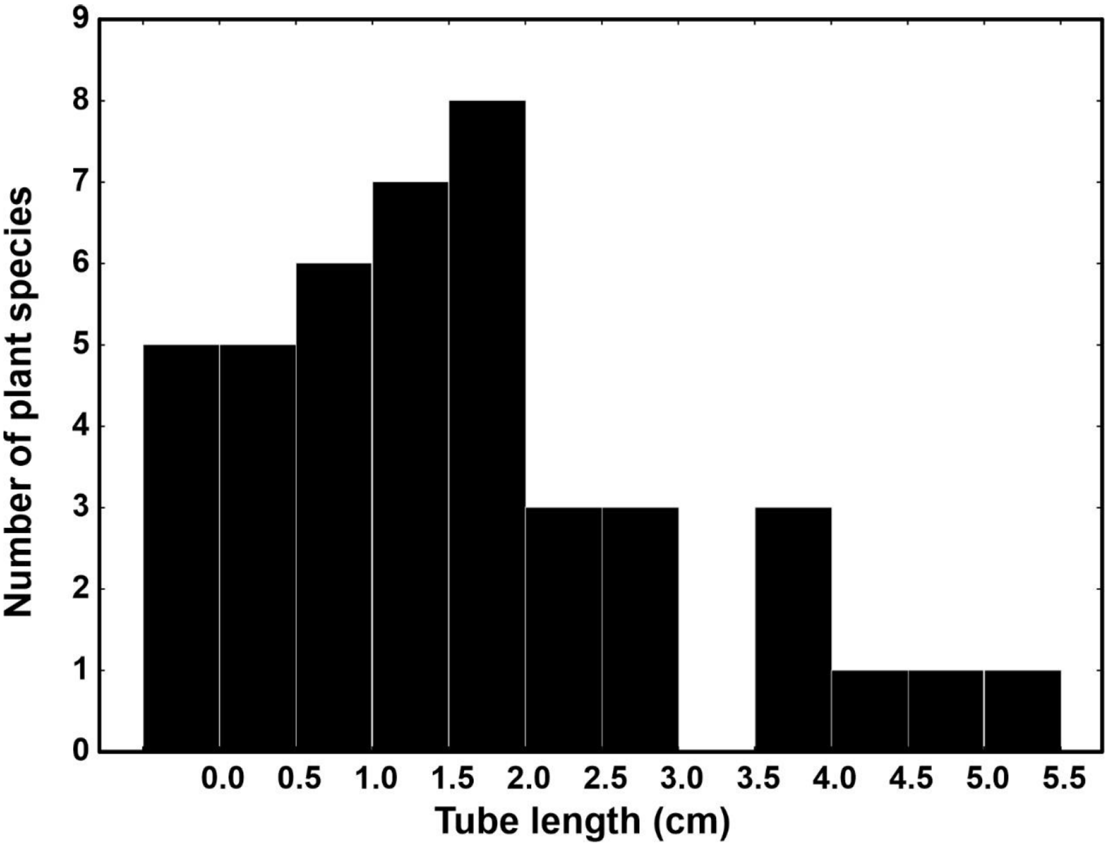

Figure S4. Distribution of floral lengths in the sunbird visited plant species.

Table S1. Details of the sampling localities and year of sampling. Each sampling site was sampled in two distinct seasons: dry and wet.

Site	Coordinates	Elevation (m a.s.l.)	Description	Sampling year
PlanteCam Camp	N 04.1175º, E 09.0717º	1100	Mid-elevation forest, partly disturbed by elephants, where *Kigelia africana*, *Macaranga occidentalis, Trichilia rubescens, Drypetes leonensis* and *Voacanga africana* are common.	2018-2019
Crater Lake	N 04.1443º, E 09.0709º	1500	Submontane forest, highly disturbed by elephants. In the forest patches are common trees such as *Tabernaemontana ventricosa*, *Anthonontha fragrans*, *Allophylus bullatus*, *Xylopia africana* and *Dicranolepis vestita*. Large elephant pastures are often dominated by grasses and *Aframomum* spp.	2019-2020
Mann's Spring	N 04.1428º, E 09.0630º	2100	Montane forest, close to the timberline, where elephant disturbance is absent and where montane species like *Syzigium staudtii*, *Nuxia congesta* and *Astropanax* spp. are common.	2019-2020
Hut 1	N 04.1759 º, E 09.2041 º	2100	Low-elevational grasslands are relatively species-poor communities dominated by tall grasses, *Cenchrus monostigma*, and *Loudetia simplex*. There are not many species specific for these grasslands e.g. *Habenaria mannii*. In these communities, we can also find herbs (e.g. *Lobelia columnaris*) or scattered trees (e.g. *Nuxia congesta*) that occur in the montane forest.	2021-2022
Hut 2	N 4.1938 º, E 09.1938 º	2800	High-elevation grasslands are species-rich grasslands with a common occurrence of grasses, such as *Andropogon* spp., *Sporobolus montanus, and Koeleria capensis*. Taller vegetation with *Phyllopentas schimperi* or *Hypericum revolutum* can be found locally in leeward areas.	2021-2022

Table S2: Observation effort for individual plant species.

Camp	Season	Observation	Species	Observation time (hrs.)
PLANTECAM CAMP	dry	camera	*Brillantaisia owariensis*	224.5
PLANTECAM CAMP	dry	camera	*Costus dubius*	205.6
PLANTECAM CAMP	dry	camera	*Impatiens niamniamensis*	240.4
PLANTECAM CAMP	dry	personal	*Kigelia africana*	60.2
PLANTECAM CAMP	dry	personal	*Mussaenda tenuiflora*	119.6
PLANTECAM CAMP	dry	personal	*Tabernaemontana ventricosa*	70
PLANTECAM CAMP	wet	camera	*Costus dubius*	117.8
PLANTECAM CAMP	wet	camera	*Impatiens etindensis*	91.2
PLANTECAM CAMP	wet	camera	*Impatiens frithii*	153.3
PLANTECAM CAMP	wet	camera	*Impatiens hians*	124.3
PLANTECAM CAMP	wet	camera	*Impatiens niamniamensis*	121.8
PLANTECAM CAMP	wet	camera	*Plectranthus decurrens*	53.4
PLANTECAM CAMP	wet	camera	*Thonningia sanguinea*	123.7
PLANTECAM CAMP	wet	camera	*Thunbergia fasciculata*	107.4
PLANTECAM CAMP	wet	personal	*Mussaenda tenuiflora*	71.6
CRATER LAKE	dry	camera	*Acanthopale decempedalis*	226.3
CRATER LAKE	dry	camera	*Aframomum sp. white*	210.4
CRATER LAKE	dry	camera	*Brillantaisia owariensis*	222.9
CRATER LAKE	dry	camera	*Costus dubius*	170.6
CRATER LAKE	dry	camera	*Hypoestes triflora*	235.1
CRATER LAKE	dry	camera	*Impatiens burtonii*	258.4
CRATER LAKE	dry	camera	*Impatiens niamniamensis*	212.1
CRATER LAKE	dry	camera	*Ixora guineensis*	24
CRATER LAKE	dry	camera	*Mimulopsis solmsii*	225.1
CRATER LAKE	dry	camera	*Plectranthus kamerunensis*	219.8
CRATER LAKE	dry	camera	*Thonningia sanguinea*	93.5
CRATER LAKE	dry	personal	*Dicranolepis vestita*	64
CRATER LAKE	dry	personal	*Englerina gabonensis*	64
CRATER LAKE	dry	personal	*Kigelia africana*	64
CRATER LAKE	dry	personal	*Mussaenda tenuiflora*	64
CRATER LAKE	dry	personal	*Psydrax dunlapii*	64
CRATER LAKE	dry	personal	*Syzygium sp.*	64
CRATER LAKE	dry	personal	*Tabernaemontana ventricosa*	64
CRATER LAKE	wet	camera	*Acanthopale decempedalis*	242.8
CRATER LAKE	wet	camera	*Aframomum sp. white*	106.9

CRATER LAKE	wet	camera	*Clerodendrum silvanum*	246
CRATER LAKE	wet	camera	*Costus dubius*	135.1
CRATER LAKE	wet	camera	*Impatiens burtonii*	111.1
CRATER LAKE	wet	camera	*Impatiens etindensis*	232.8
CRATER LAKE	wet	camera	*Impatiens niamniamensis*	238.5
CRATER LAKE	wet	camera	*Ixora guineensis*	138
CRATER LAKE	wet	camera	*Plectranthus kamerunensis*	88.8
CRATER LAKE	wet	camera	*Rhipidoglossum sp*	88.9
CRATER LAKE	wet	camera	*Thonningia sanguinea*	230.6
CRATER LAKE	wet	personal	*Anthocleista scandens*	64
CRATER LAKE	wet	personal	*Mussaenda tenuiflora*	62
MANN’S SPRING	dry	camera	*Acanthopale decempedalis*	216.8
MANN’S SPRING	dry	camera	*Hypoestes triflora*	223.5
MANN’S SPRING	dry	camera	*Impatiens sakeriana*	218.6
MANN’S SPRING	dry	personal	*Clausena anisata*	64
MANN’S SPRING	dry	personal	*Ixora foliosa*	68
MANN’S SPRING	dry	personal	*Nuxia congesta*	64.1
MANN’S SPRING	dry	personal	*Psydrax dunlapii*	64
MANN’S SPRING	dry	personal	*Astropanax abyssinicum*	65.1
MANN’S SPRING	dry	personal	*Syzygium staudtii*	64
MANN’S SPRING	wet	camera	*Acanthopale decempedalis*	211.3
MANN’S SPRING	wet	camera	*Impatiens sakeriana*	160.9
MANN’S SPRING	wet	camera	*Jasminum preussii*	202.4
MANN’S SPRING	wet	camera	*Psychotria peduncularis var. hypsophila*	251.5
MANN’S SPRING	wet	camera	*Rhipidoglossum sp.*	167.2
HUT 1	dry	personal	*Hypericum revolutum*	273.2
HUT 1	dry	personal	*Leucas oligocephala*	16.1
HUT 1	dry	personal	*Lobelia columnaris*	184.95
HUT 1	dry	personal	*Nuxia congesta*	8.05
HUT 1	dry	personal	*Phyllopentas schimperi*	102.45
HUT 1	dry	personal	*Clinopodium robustum*	236.95
HUT 1	wet	personal	*Hypericum revolutum*	177.65
HUT 1	wet	personal	*Phyllopentas schimperi*	178.57
HUT 2	dry	personal	*Lasiosiphon glaucus*	88.3
HUT 2	dry	personal	*Hypericum revolutum*	176.6
HUT 2	dry	personal	*Phyllopentas schimperi*	137.23
HUT 2	dry	personal	*Rhabdotosperma densifolia*	22.22
HUT 2	dry	personal	*Clinopodium robustum*	329.07
HUT 2	dry	personal	*Succisa trichotocephala*	201.98
HUT 2	wet	personal	*Clematis simensis*	97.17
HUT 2	wet	personal	*Hypericum revolutum*	266.13

HUT 2	wet	personal	*Leucas oligocephala*	205.07
HUT 2	wet	personal	*Phyllopentas schimperi*	411.28
HUT 2	wet	personal	*Rhabdotosperma densifolia*	128.72
HUT 2	wet	personal	*Clinopodium robustum*	376.92
HUT 2	wet	personal	*Solanum pseudospinosum*	121.85
HUT 2	wet	personal	*Succisa trichotocephala*	140.8

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PLANT-MICROBE-ANIMAL INTERACTIONS – ORIGINAL RESEARCH

Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon

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Abstract

Differences in interaction specializations between nectarivorous birds and plants across continents serve as common examples of evolutionary trajectory specificity. While New World hummingbird-plant networks have been extensively studied and are considered highly specialized, knowledge on the network specialization of their Old World counterparts, sunbirds (Nectariniidae), remains limited. A few studies from tropical Africa indicate that sunbird-plant networks are rather generalized. Unfortunately, these studies are limited to dry seasons and high elevations at the tree line, environments where niche-based hypotheses also often predict lower resource partitioning. In our study, we explored the specialization of sunbird-plant networks and their spatiotemporal variability on Mt. Cameroon (Cameroon). Using a combination of automatic video recordings and personal observations, we constructed eight comprehensive sunbird-plant networks in four forest types at different elevations in both the dry and wet seasons. As reported in previous studies, the montane forest plants, birds and whole networks were highly generalized. Nevertheless, we observed a much higher specialization in forests at lower elevations. Except at the lowest altitude, the wet season was also characterized by higher specialization. While less specialized flowering trees dominated in the dry season networks, more specialized herbs and shrubs were visited by birds during the wet season. As our findings do not support the generally accepted assumption that Old World bird-plant networks are rather generalized, we need further studies to understand the differences in bird-plant specializations on individual continents.

Keywords Bird pollination · Ecological network · Elevation · Sunbird · Seasonality

Introduction

Specialization of plant-pollinator networks is a fundamental ecosystem characteristic. Knowledge on this specialization and how it is affected by various environmental conditions is significant from many points of view. It is important not only for conservation purposes (e.g., for estimating the extinction risk of individual organisms, Vanbergen et al. 2017) and for predicting the effects of future climate changes on plant-pollinator communities (Hoiss et al. 2015) but also for a general understanding of evolutionary and speciation processes (Ramírez et al. 2011).

Specialization in plant-pollinator networks reflects resource (niche) partitioning among species, which can be driven by the tendency of plants and pollinators to use only a subset of potential resources and by interplant or inter-pollinator interactions such as competition (Blüthgen et al. 2006). Some of the most studied networks are those among plants and nectarivorous birds. Nevertheless, whereas researchers have often targeted hummingbird-plant interactions, networks including other groups of nectarivorous birds remain underexplored. A few studies on African sunbird-plant networks indicate that they are less specialized than hummingbird-plant networks (Zanata et al. 2017; Nsor et al. 2019). Nevertheless, other studies revealed many similarities that should result in a similar degree of specialization. For

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example, it is generally accepted that both hummingbirds and sunbirds are similarly specialized for nectarivory in many traits, such as bill length, tongue structure or digestive tract functioning (Stiles 1981). Even the ability to hover, which was considered to be unique to hummingbirds for a long time (Stiles 1981; Fleming and Muchhala 2008), was documented in sunbirds (Geerts and Pauw 2009a; Wester 2014). Moreover, plants adapted to hovering sunbirds also occur in the African tropics (Janeček et al. 2011; Bartoš and Janeček 2014; Sejfová et al. 2021) and sunbirds also drive insects away from food plants in their territories (Ollerton and Nuttman 2013; Tropek et al., 2013), as hummingbirds do (Jacobi and Antonini 2008). In both bird groups, we found a high variability in morphological and behavioural nectarivory-related traits, such as bill length, bill curvature or ability to hover, which enable resource partitioning (Paton and Collins 1989; Janečková et al. 2021; see also Adler et al. 2013). Resource partitioning itself was also documented in both hummingbird and sunbird assemblages composed of species with different functional traits (Feinsinger et al. 1985; Geerts and Pauw 2009b; Janeček et al. 2012). Considering plants, a wide spectrum of growing forms and degrees of specialization (Fleming and Muchhala 2008) were recorded in both American and African flora. Hummingbirds and sunbirds interact with nonspecialized plant species, often canopy trees (Maruyama et al. 2014; Nsor et al. 2019; Chmel et al. 2021), and also with highly specialized ornithophilous plants, often herbs, shrubs, and epiphytes (Cronk and Ojeda 2008; Janeček et al. 2015; Chmel et al. 2021). Resource (i.e., avian pollinator) partitioning among plant species was documented in both systems (Stiles 1981).

There are several studies on the factors affecting the specialization of nectarivorous bird-plant interaction networks; however, almost all of them focus on hummingbird-plant networks (e.g., Maglianesi et al. 2014; Cuartas-Hernández and Medel 2015; Maruyama et al. 2018). The observed pattern along elevational gradients, which serve as exceptional field laboratories characterized by rapid environmental changes, differs depending on the metrics used and the location being studied. Using the species-level specialization index (d´), which determines how the resource use of a particular plant or pollinator differs from opportunism (i.e., usage of the resources proportional to their abundance), Maglianesi et al. (2015) showed a greater specialization of hummingbirds at low (0 m a.s.l.) and middle (1,000 m a.s.l.) elevations compared to high elevations (2,000 m a.s.l.). In the same study area, the complementarity specialization index (H'_2), which considers both plant and visitor specialization and determines network-level niche partitioning, was the highest at middle elevations (Maglianesi et al. 2014). In contrast, Partida-Lara et al. (2018) demonstrated, on a similarly long elevational gradient, that the highest complementary specialization is found at high elevations. Sonne et al. (2019) showed a more complex pattern along a more expansive elevational gradient (0–4,000 m a.s.l.), where there was a dominance of curved-bill specialists in the lowlands, long-straight bill specialists at high elevations and relatively low hummingbird species level specialization at middle elevations. In contrast, Pellissier et al. (2017) demonstrated a decrease in hummingbird-plant network connectance (i.e., an increase in specialization) at high elevations.

Studies on the temporal variability of bird-plant network specialization are rather rare. Partida-Lara et al. (2018) found similar complementarity specialization in hummingbird networks across a one-year period. Maruyama et al. (2014) found that plant and hummingbird phenological overlap is important for network modularity (i.e., the occurrence of specialized parts, a.k.a. modules, of the network where some group of plants and pollinators interact more frequently with each other than with the other members of the network). Nevertheless, many studies not directly targeting plant-bird networks presented various phenological patterns that should be reflected in temporal changes in network specialization. Independent studies demonstrated that flowering intensity and nectar availability for birds could vary considerably from season to season, not only for hummingbirds (Wolf 1970; Araujo and Sazima 2003; Abrahamczyk and Kessler 2010) but also for sunbirds (Collins and Rebelo 1987) and honeyeaters (Collins and Briffa 1982; Collins 1985; Comer and Wooller 2002). Specific flowering patterns of individual plant groups can also contribute to these patterns. For example, tropical trees (Janzen 1967; Bentos et al. 2008) and specialized ornithophilous herbs can predominantly bloom in certain seasons of the year (Janeček et al. 2015). In contrast, the dry season can be characterized by many open actinomorphic flowers (Klomberg et al. 2022). Unfortunately, all published sunbird-plant networks from tropical Africa were studied in the dry season (Janeček et al. 2012; Zanata et al. 2017; Nsor et al. 2019). We suspect that this might greatly bias our general conclusions on sunbird-plant interactions.

Here, we aim to explore the specialization of sunbird-plant interactions on Mt. Cameroon, the highest peak of West Africa. We specifically explored the sunbird-plant networks in different forest types occurring at different elevations and in two contrasting seasons (wet and dry). Our goal was to focus on two main questions and to test related hypotheses: (1) Are birds, plants and whole networks at higher elevations more or less specialized? We hypothesized that at higher elevations, there would be lower specialization, possibly due to lower plant and bird diversities and lower resource partitioning in harsher and less predictable environments. In contrast, we expected higher specialization in more diverse lowlands with more stable environmental conditions (Rasmann et al. 2014). Nevertheless, arguments against this hypothesis can also be found in the literature. For example, birds are relatively better pollinators than insects in cold weather, and consequently, there can be more specialized bird-pollinated plants, which enables better niche separation at higher elevations (Cruden 1972; Huang et al. 2017). (2) Are the birds, plants and whole networks more specialized in the wet season? We hypothesized that a higher specialization can be expected, as many specialized ornithophilous plants bloom only in the wet season (Cruden 1972; Janeček et al. 2015), which can enable more precise niche segregation in that season (Abrahamczyk and Kessler 2010). Higher specialization can also be driven by lower nectar availability, as observed in hummingbird-plant networks (Tinoco et al. 2017).

Materials and methods

Study site

Our study was performed on the southwestern slope of Mt. Cameroon (Cameroon, Fig. 1), which is the highest mountain of West-Central Africa (4,040 m a.s.l.) and an important biodiversity hotspot (Küper et al. 2004). The lowest elevations of the southwestern slope are used for plantations, but from approximately 400 m a.s.l. to the treeline (2,200 m a.s.l.), there is a primary tropical forest habitat (Cable and Cheek 1998). The temperature and precipitation decrease with increasing elevation (Maicher et al. 2020) together with the diversities of plants and birds (Hořák et al. 2019). The

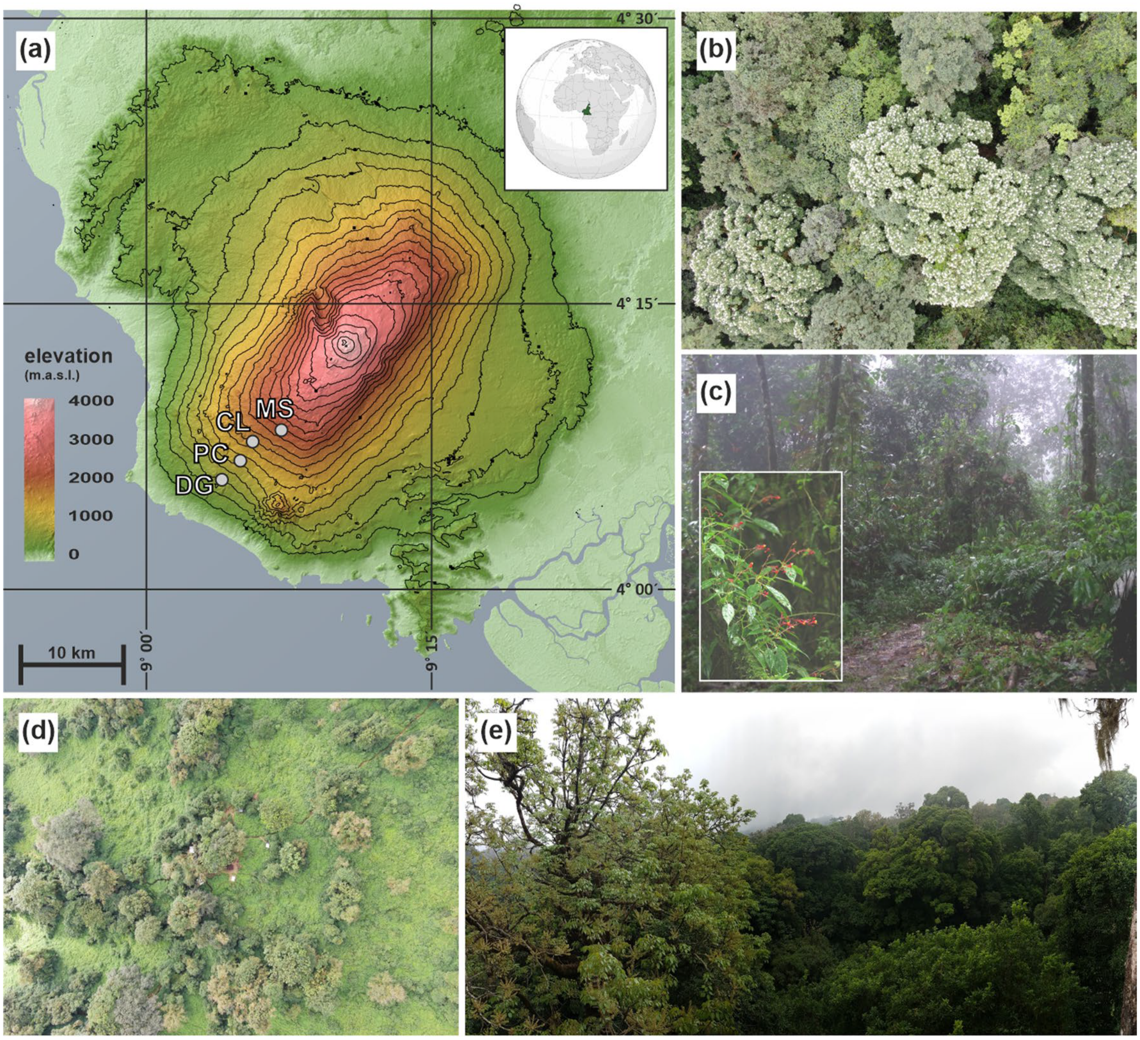


Fig. 1 Study sites on Mt. Cameroon. **a** Mt. Cameroon. *DG*—Drink Gari, *PC*—PlanteCam Camp; *CL*—Crater Lake; *MS*—Mann's Spring. **b** Lowland forest around DG in the dry season. Whitish trees are *Berlinia bracteosa* in flower. **c** Mid-elevation forest around PC; *Impatiens frithii*, a flowering epiphytic ornithophilous species, is seen in the frame. **d** Submontane forest around CL with large patches of herbaceous vegetation maintained by forest elephants. (e) Montane forest in the dry season near MS. The tree on the left-hand side is a flowering *Schefflera abyssinica*

study was performed in four forest types: (1) Lowland forest (LF) in the Drink Gari locality (650 m a.s.l.), which is only slightly disturbed by elephants and where members of the plant subfamily Caesalpiniaceae (family Fabaceae) are common; (2) Mid-elevation forest in the PlanteCam camp locality (1,100 m a.s.l.), which is partly disturbed by elephants with common occurrence of *Kigelia africana*, *Macaranga occidentalis* and *Voacanga africana*; (3) Submontane forest in the Crater Lake locality (1,500 m a.s.l.), which is strongly disturbed by elephants and is consequently mixed with large elephant pastures with common occurrence of *Aframomum* spp.; and 4) Montane forest around Mann's Spring (2,200 m a.s.l.) close to the treeline, which lacks elephant disturbance and has occurrence of montane species such as *Syzygium staudtii*, *Nuxia congesta* or *Schefflera* spp. (Fig. 1). Data were collected during four expeditions across three years. The first expedition was organized in 2018, the second and third in 2019 and the last in 2020. During each expedition, we collected data from two sites (i.e., forest types). Thus, the data were collected during two expeditions to each site, one in the dry season (end of January to mid-March) and one in the wet season (end of July to mid-September). Six transects (200 m long and 10 m wide, at least 100 m apart) were established at each site (i.e., 24 transects in total), and the abundance of plants in bloom within each transect was counted. Counting was performed in each transect once during the plant-sunbird observations, i.e., plants were counted twice in each transect, once in the dry season and once in the wet season. We defined the following plant growth forms: (1) *herbs*; non-woody plants without vertical support from other plants, (2) *lianas*; plants using vertical support of other plants, (3) *shrubs*; non-climbing woody plants up to 5 m high rooting on the ground, (4) *trees*; non-climbing woody plants often higher than 5 m, (5) *parasitic shrubs*; woody plants growing in the canopies of trees (members of the Loranthaceae family in our dataset).

Observations of sunbird-plant interactions

We considered each individual plant as one observation unit. For lianas, where determining an individual in the field was impossible, we defined individuals as those plants that had flowering parts that were not obviously connected to another flowering part. We considered individual plant species to be potentially bird-visited if the nectar amount in a covered flower after 24 h was higher than 0.3 µl/per flower (unpublished data, see also Janeček et al. 2021), if it flowered in at least three replicates on the six transects, or if it occurred less frequently but was commonly flowering outside the transects. Sunbird-plant interactions were observed using two complementary methods. The first method utilised security cameras (Vivotek IB8367RT) to observe herbs and small shrubs. We aimed to record 10 individuals of each plant species and each individual for 2 days (from 6 am to 6 pm). If there were not enough replicates on the transect, the plants were observed out of transects. The rarity of some species, together with logistical and/or technical problems related to the harsh weather of Mt. Cameroon, resulted in different total recording times for individual plants (Table S1). Finally, the mean video observation period was 152 h per plant species. Floral visitors were identified in the videos either manually or using the automatic movement detection software MotionMeerkat (Weinstein 2015). The second method was the direct observation of trees and tall shrubs (i.e., those that were not suitable for the camera's field of view). We aimed to observe eight individuals per plant species, each of them for 8 h distributed equally throughout the day. As we could not always find a sufficient number of individuals, the mean observation time per species was 68 h (Table S1). Tall trees were usually observed from a neighbouring tree, on which the observer climbed using a single-rope climbing technique. During direct observations, it was not always possible to recognize whether the birds touched the reproductive organs of the plant. Consequently, we considered all visits as one kind of interaction, i.e., without considering if they resulted in plant pollination or if the birds were just feeding. We considered the time from the bird's arrival until its departure as one event. Birds were not banded, so we were unable to distinguish individual birds.

Assessment of interaction abundances

We quantified plant abundance to estimate the total number of interactions in the studied area. To do this, we counted all flowering individual plants inside six 200 × 10 m transects at each site during each expedition, giving us data on flowering plant abundance from 1.2 hectares. The values in individual cells of bird-plant interaction matrices were then calculated as the visitation frequency per plant per hour multiplied by plant abundance per hectare. Consequently, the interaction strength was considered at the ecosystem level, i.e., it expressed how many interactions between specific bird and plant species per hour we could observe in one hectare of forest. Nevertheless, in the supplementary material, results are also shown for interactions that were not considered per hectare but only as the frequency of visits per plant (Table S2, Table S3). We constructed eight networks corresponding to four elevations and two seasons, i.e., the information from transects (and the plants observed out of transects) from one season and elevation were merged to build one network. The visitation frequencies per hour were often low (< 1). To achieve the integer values needed for calculations of some specialization indices, the frequencies per hour and hectare were arbitrarily multiplied by 10,000 and rounded up. For plants that were relatively common but did not appear on transects, we arbitrarily set their abundance as

1 individual per 2 hectares. The data on interaction networks are available in Supplementary file 2.

Specialization metrics

To describe the specialization of sunbird plant networks, we used current standard indices, most of which were also used in the most complex worldwide study on specialization in nectarivorous bird-plant networks (Zanata et al. 2017). At the species level, we calculated Blüthgen´s standardized species specialization (*d′*) (Blüthgen et al. 2006) and the normalized degree (ND) (Freeman 1979) for sunbirds and plants. The index *d′* is related to Shannon diversity and compares the distribution of the interactions with each partner to the overall partner availability and it ranges from 0 (max. generalization) to 1 (max. specialization). The ND is simply the proportion of species that a species interacts with out of the total possible number of species in the network (Freeman 1979; González et al. 2010). At the network level, we used connectance (C), which is the proportion of realized to all possible interactions in the network, complementary specialization ($H_2´$), which is a generalization of d´ for the whole network and similarly ranges from 0 (fully generalized) to 1 (max. specialized) (Blüthgen et al. 2006; González et al. 2015), and Newman´s weighted modularity measure (**Q**) that compares the density of the connections inside and between the modules. Q ranges from 0 for randomly arranged networks to 1 for networks with perfectly defined modules (Newman 2004, 2006; Dormann and Strauss 2014). The modules were detected using Beckett's algorithm (Beckett 2016). Note that in our interaction networks, we did not use the real numbers of observed interactions but estimated numbers of interactions per area (one hectare).

Sampling completeness

To estimate the effect of sampling effort on the studied specialization metrics, we used a rarefaction-like approach based on Vizentin-Bugoni et al. (2016) and Dehling et al. (2014). From each network dataset, we incrementally removed a proportion of the data and calculated the specialization index each time. At each step, we removed 5% of the dataset; i.e., 5% of the minutes of observations (rows in the dataset) were randomly selected for removal. The same proportion of rows was removed for each observed plant species. At each step, random data removal was performed one thousand times.

Statistical analyses

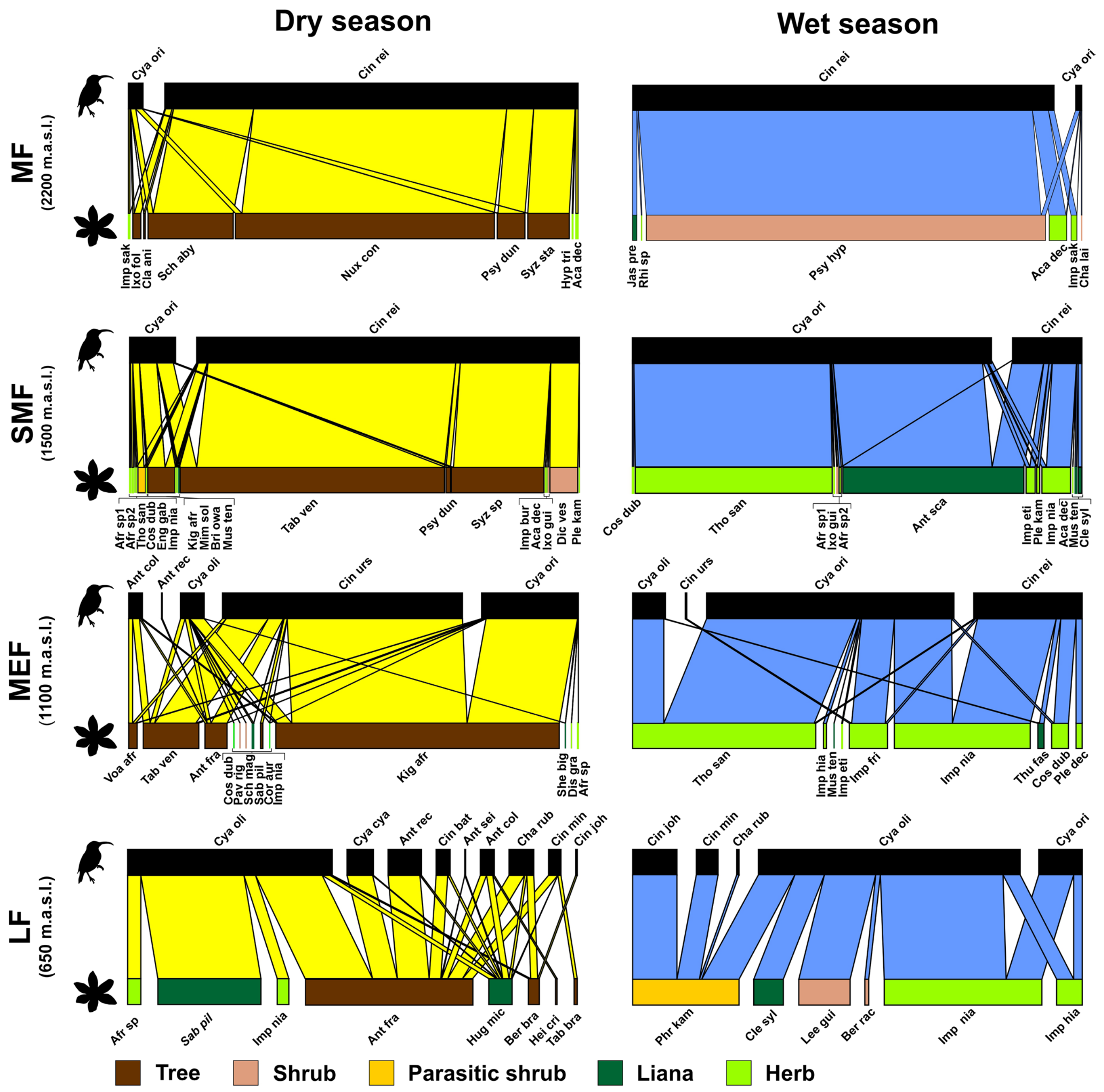
The plant-growth form × season or plant-growth form × elevation contingency tables containing count data on plant species affiliated to individual growth-forms were tested using Fisher's exact test in R (R Core Team, 2020).

Specialization indices were calculated using the package bipartite 2.15 (Dorman et al. 2008) in R 4.0.0 (R Core Team 2020). Because the values of some species-level indices were not normally distributed, we used a nonparametric permutation ANOVA for statistical analyses of plant and sunbird specializations in individual forest types and seasons. Elevation and season were treated as fixed factors. Permutation tests were performed using the PERMANOVA + program for PRIMER (Anderson et al. 2008). These analyses are nearly identical to the traditional ANOVA. The small difference is that the *F* ratio in the permutation ANOVA does not have a known distribution under the true null hypothesis, and consequently, it is denoted as pseudo F ($F_{ps.}$). The permutation P value ($p_{\mathrm{perm.}}$) is calculated as the proportion of $F_{\mathrm{ps.}}$ values achieved by permutations that are greater than or equal to the observed $F_{\mathrm{ps.}}$

The observed values of the network-level matrices H_2' and Q were tested by comparison with null models. The values for the null models were computed from 1,000 networks generated by the Vaznull algorithm (Vázquez et al. 2007). The Vaznull algorithm is relatively conservative, preserves the connectance, and moderately preserves the marginal totals of the observed network. Consequently, it is often considered to be more realistic than other algorithms (e.g., Patefield's algorithm) because it more accurately reflects some natural constraints in network architectures, such as the impossibility of some links (forbidden links) due to trait mismatches or phenological shifts (e.g., Figueroa et al. 2020).

Results

In total, plants were observed for 15,767 h and 8205 sunbird-plant interactions were recorded. We observed 12 sunbird species interacting with 49 plant species. The number of interacting sunbirds differed at different elevations (Fig. 2). The highest number of sunbirds (9 species) was observed in the lowland forest in the dry season. In contrast, only two sunbird species visited plants in the submontane and montane forests. The numbers of visited plants were higher in the mid-elevation, submontane forests and in the dry season (Fig. 2). The plant growth-form spectrum of visited plant species differed between dry and wet seasons (Fisher's exact test, $p < 0.001$). Trees were the most visited growth form in the dry season, whereas the majority of visited plant species in the wet seasons were herbs (Fig. 2). No differences were observed among elevations in the dry (Fisher's exact test, $p = 0.396$) and wet (Fisher's exact test, $p = 0.361$) seasons. Nevertheless, some lianas (*Sabicea pilosa* and *Hugonia micans*) were among the most visited plant species in the



dry season in lowland forest and shrub *Psychotria hypsophila* was the most visited plant species in the wet season in the montane forest. The species-level sunbird specialization (d') significantly differed among elevations (Table 1). We detected the lowest sunbird d' specialization in the mountain forest, whereas the specialization was higher at lower elevations (Fig. 3a). The normalized degree differed among forest types, with the highest values in montane and submontane forests (Table 1, Fig. 3b). The species-level plant specialization (d') significantly differed among individual forest types (Table 1). Plant specialization was highest in the lowland forest network and decreased at higher altitudes (Fig. 3c). The opposite pattern was found for the normalized degree of plants, which was lowest at low elevations and highest at high elevations (Table 1, Fig. 3d).

The lower specialization at high elevations was also obvious when considering the network-level indices. Connectance (C) was higher in the two upper forest types (Table 2). Both the observed complementary specialization (H_2') and modularity (Q) were much lower in mountain forests. H_2' and Q significantly differed from the values predicted by the null models in all but one network, indicating that the networks were specialized and modular (Table 2). The only exception was the wet season network

◂**Fig. 2** Sunbird-plant networks on Mt. Cameroon at four elevations in dry and wet seasons. LF – lowland forest; MEF – mid-elevation forest; SF – submontane forest; MF – montane forest. **PLANTS**: ***Aca dec***—*Acanthopale decempedalis*; ***Afr sp.***—*Aframomum sp.*; ***Ant sca***—*Anthocleista scandens*; ***Ant fra***—*Anthonotha fragrans*; ***Ber bra***—*Berlinia bracteosa*; ***Ber rac***—*Bertiera racemosa*; ***Bri owa***—*Brillantaisia owariensis*; ***Cha lai***—*Chassalia laikomensis*; ***Cla ani***—*Clausena anisata*; ***Cle syl***—*Clerodendrum sylvanum*; ***Cos dub***—*Costus dubius*; ***Cor aur***—*Cordia aurantiaca*; ***Dic ves***—*Dicranolepis vestita*; ***Dis gra***—*Dischistocalyx grandiflora*; ***Eng gab***—*Englerina gabonensis*; ***Hei cri***—*Heinsia crinita*; ***Hug mic***—*Hugonia micans*; ***Hyp tri***—*Hypoestes triflora*; ***Imp bur***—*Impatiens burtonii*; ***Imp hia***—*Impatiens hians var. hians*; ***Imp eti***—*Impatiens etindensis*; ***Imp fri***—*Impatiens frithii*; ***Imp nia***—*Impatiens niamniamensis*; ***Imp sak***—*Impatiens sakeriana*; ***Ixo fol***—*Ixora foliosa*; ***Ixo gui***—*Ixora guineensis*; ***Jas pre***—*Jasminum preussii*; ***Kig afr***—*Kigelia africana*; ***Lee gui***—*Leea guineensis*; ***Mim sol***—*Mimulopsis solmsii*; ***Mus ten***—*Mussaenda tenuiflora*; ***Nux con***—*Nuxia congesta*; ***Pav rig***—*Pavetta rigida*; ***Phr kam***—*Phragmanthera kamerunensis*; ***Ple dec***—*Plectranthus decurrens*; ***Ple kam***—*Plectranthus kamerunensis*; ***Psy hyp***—*Psychotria hypsophila*; ***Psy dun***—*Psydrax dunlapii*; ***Rhi sp.***—*Rhipidoglossum sp.*; ***Sab pil***—*Sabicea pilosa*; ***Sch mag***—*Schumanniophyton magnificum*; ***Sch aby***—*Schefflera abyssinica*; ***Syz sta***—*Syzygium staudtii*; ***Syz sp.***—*Syzygium sp.*; ***Tab bra***—*Tabernaemontana brachyantha*; ***Tab ven***—*Tabernaemontana ventricosa*; ***Tho san***—*Thonningia sanguinea*; ***Thu fas***—*Thunbergia fasciculata*; ***Voa afr***—*Voacanga africana*; **SUNBIRDS**: ***Ant col***—*Anthodiaeta collaris*; ***Ant rec*** – *Anthreptes rectirostris*; ***Ant sei***—*Anthreptes seimundi*; ***Cha rub***—*Chalcomitra rubescens*; ***Cin bat***—*Cinnyris batesi*; ***Cin joh***—*Cinnyris johannae*; ***Cin min***—*Cinnyris minullus*; ***Cin urs***—*Cinnyris ursulae*; ***Cin rei***—*Cinnyris reichenowi*; ***Cya cya***—*Cyanomitra cyanolaema*; ***Cya oli***—*Cyanomitra olivacea;* ***Cya ori***—*Cyanomitra oritis*

in the lowland forest, where there was an insignificant difference between the observations and the null model's prediction of complementary specialization. H_2' had higher values at all elevations in the wet season (Table 2). The results and conclusions did not differ much when considering the interaction strength as the number of visits per plant (i.e., not per hectare, Table S2, Table S3, Fig. S1), and the d' values calculated from hectare- and plant individual-based networks were positively correlated (Fig. S2). Analyses on possible sampling incompleteness revealed that the values of many parameters showed little variability when only 40–60% of the original dataset was used (Figs. S3′S9). The lowest parameter stability was observed in the smallest network from the mountain forest in the wet season. For the randomly selected data subsets of this network and their resulting index values, it was important whether the rare interactions of *Cyanomitra oritis* with *Psychotria hypsophila*, the plant that was most frequently visited by *Cinnyris reichenowi*, were selected. If these interactions were not selected, the parameters indicated a higher specialization (see Fig. S3, S4 and S8—montane forest, wet season).

Discussion

The networks presented in this study were much more specialized, irrespective of the index used, than those of the two other published studies on quantitative networks in tropical Africa (Zanata et al. 2017; Nsor et al. 2019). Nevertheless, these studies are fully consistent with our results if we consider when and where they were performed. The first was carried out in the Bamenda highlands (Cameroon) in shrubby vegetation along a small stream at an elevation of approximately 2,200 m a.s.l. (Janeček et al. 2012; Zanata et al. 2017) and the second was conducted in the montane forest on the Mambilla Plateau (Nigeria), at approximately 1650 m a.s.l. (Nsor et al. 2019). Moreover, both studies were performed in the dry season. Our montane, dry season network was also characterised by a substantially lower specialization than other networks.

The differences between our high network-level specialization and the lower specialization of networks in South Africa, measured as H_2', Q or C (Zanata et al. 2017), can be explained by three hypotheses, all of which warrant testing in the future. This low specialization in South African studies can result from: (1) the latitudinal pattern and specialization decrease towards higher latitudes where a smaller number of organisms can occupy larger niches (MacArthur 1968), but this hypothesis is still contentious (e.g., Ollerton and Cranmer 2002); (2) the specific properties of Austro-temperate flora in South Africa, which is closely related to the flora of Australia (Linder 2014). For example, this flora has a very high number of ornithophilous plants per sunbird species (Rebelo 1987; Geerts and Pauw 2009b); or (3) the sampling method, as all the studies from South Africa evaluated by Zanata et al. (2017) were constrained by the sampling of a targeted subset of plants in the community, e.g., *Salvia* and *Lycium* (Wester 2013), *Protea* (Schmid et al. 2016) or *Aloe* (Botes et al. 2008).

Our findings from the montane forest were consistent with other pollination network studies that showed the lowest number of potential visitors (Ramos-Jiliberto et al. 2010) and both a lower group- (Miller-Struttmann and Galen 2014) and network-level (Hoiss et al. 2015) specialization at high elevations. The same pattern has also been demonstrated in hummingbird-plant networks (Maglianesi et al. 2015). However, this distribution of specialization patterns is not consistently observed in hummingbird networks. For example, Partida-Lara et al. (2018) revealed the opposite pattern (i.e., the lowest specialization at low elevations), suggesting that local conditions are important. Their study was performed on a gradient with different vegetation types at different sampling elevations, with the lowest number of interacting species found in

Table 1 Effect of season and forest type on bird and plant specialization, expressed as Blüthgen's specialization index (d') and normalized degree (ND)

	Bird $d´$		Bird ND		Plant d'		Plant ND	
	F_{ps}	p_{perm}	F_{ps}	p_{perm}	F_{ps}	p_{perm}	F_{ps}	p_{perm}
Season	2.34	0.145	0.19	0.667	0.01	0.916	0.50	0.487
Forest	4.18	0.012*	5.27	0.004**	4.85	0.004**	12.72	0.001**
Forest*season	0.50	0.689	0.14	0.926	1.55	0.224	0.32	0.790

Permutation ANOVA * $0.01 < p < 0.05$; ** $p < 0.01$

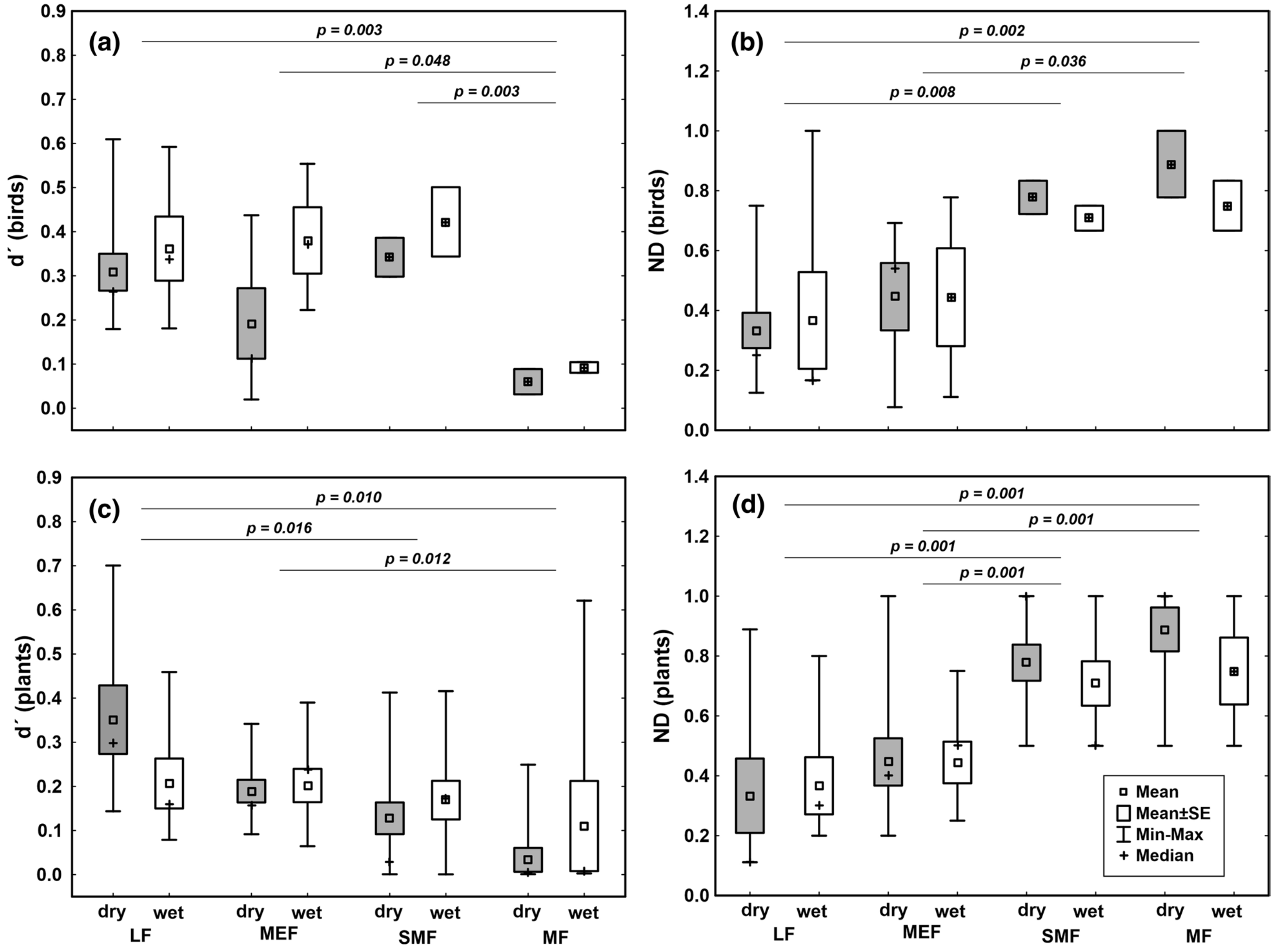


Fig. 3 Specialization of birds (**a**, **b**) and plants (**c**, **d**) in the individual forest types on Mt. Cameroon. d'—Blüthgen´s specialization index; ND—normalized degree. Significant pairwise differences between individual forest types are reported. LF—lowland forest; MEF—mid-elevation forest; SF—submontane forest; MF—montane forest

Table 2 Network-level specialization indices and their differences from the null models (Δ values) for networks in individual forest types and seasons

	Lowland forest		Mid-elevation forest		Submontane forest		Mountain forest	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
$H2'_{OBS}$	0.40**	0.43	0.17**	0.48**	0.37**	0.66**	0.08**	0.10**
Δ H2′	0.28	0.13	0.16	0.40	0.37	0.64	0.08	0.10
Q_{OBS}	0.30**	0.26*	0.10**	0.30**	0.11**	0.15**	0.02**	0.01**
ΔQ	0.23	0.15	0.09	0.25	0.11	0.14	0.02	0.01
C	0.33	0.37	0.45	0.44	0.78	0.71	0.89	0.75

lowland deciduous seasonal forest. We assume that the differences in elevational patterns between sunbird and hummingbird networks can arise from the diversification of their two, distinct phylogenetic lineages. Curve-billed hummingbirds (prevailing in the Phaethornithinae) and long-straight hummingbirds (prevailing in the Trochilinae) differ in elevational distribution and specialization, which in turn could generate a low specialization at mid elevations (Sonne et al. 2019). In contrast, although the phylogeny of sunbirds has yet to be properly resolved, groups of sunbird species do not display any obvious patterns in specialization and elevational distribution (Cheke et al. 2001).

From a niche theory perspective, our data are consistent with the altitudinal niche-breadth hypothesis in plant-pollinator interactions (Rasmann et al. 2014), which states that niches are broader in harsher montane environments. The difficulty of exploiting resources in these environments, together with harsher environmental conditions, does not necessarily underlie this pattern. Additionally, the increasing abundance of birds per species with elevation can also play a role, as was demonstrated on Mt. Cameroon (Ferenc et al. 2016). Further evidence showing that bird pollinators are generalized when they are abundant was also found by Simmons et al. (2019). Nevertheless, our data do not support the idea of a simple linear pattern along the whole gradient. The highest specialization was found in the wet season network in the submontane forest at 1500 m a.s.l. This may have resulted from the occurrence of an extremely specialized plant species, *Thonningia sanguinea*, which was almost exclusively visited by *Cyanomitra oritis* (among bird visitors) and was the most frequently visited nectar source of this sunbird. These findings support the idea that sunbirds can be effective pollinators of this species (Quintero et al. 2017). Another potentially important factor was forest disturbance. The submontane forests at these elevations were largely disturbed by elephants, and forest patches were mixed with large areas of elephant-induced clearings. Moreover, the important effects of disturbances on bird-plant networks were highlighted by Infante et al. (2020). This habitat heterogeneity and the floral richness that accompanies it (this elevation has the highest number of visited plants and number of visited plants per sunbird species) in turn facilitate a greater niche differentiation (Ebeling et al. 2011).

The seasonal comparison showed that existing assumptions on sunbird-plant network specialization in tropical Africa are likely biased, as other studies to date were performed exclusively in the dry season (Janeček et al. 2012; Nsor et al. 2019). Our study from Mt. Cameroon showed that the wet season differed from the dry season in several important aspects that potentially drove a higher wet season specialization. Herbs and parasitic shrubs are the growth forms of almost all plants with bird pollination syndrome on Mt. Cameroon (Chmel et al. 2021). The ornithophilous herbs, for example, *Impatiens* spp. (see also Janeček et al. 2015) are flowering mainly in the wet season, whereas massive flowering trees acted as significant nectar sources in the dry season (Fig. 2). The occurrence of more specialized morphologies of bird-visited herbs compared to trees may be due to the fact that herbs have shorter life cycles and can experience more rapid diversification (Snow and Snow 1972). There were also a smaller number of flowering plant individuals in the wet season, where nectar production per hectare was several times lower (unpublished data, Štěpán Janeček, Robert Tropek). It seems that the wet season is not only a much less comfortable environment for field work but also for sunbirds. Similarly, hummingbird networks showed a higher specialization under resource shortages (Tinoco et al. 2017), as has also been previously shown for whole plant-pollinator networks (Souza et al. 2018). Peaks in the number of hummingbird-visited plants were recorded in both wet (Araujo and Sazima 2003) and dry (Partida-Lara et al. 2018) seasons. As such, we need more data to determine whether this pattern is also site-specific for sunbirds. However, it is common for trees to flower in the dry season in tropical forests of various geographic areas (Janzen 1967; Nsor et al. 2019). In terms of bird-plant coevolution, we can expect that the wet season will impart much stronger selection pressures on plant and bird traits related to ornithophily or nectarivory, respectively, as there is a higher abundance of ornithophilous plants and a general lack of resources compared to the dry season. We believe that additional studies in the wet season are crucial for understanding the ecology and evolution of sunbird-plant interactions.

We agree with the opinions of other authors (e.g., Ollerton 2012) that conclusions about global patterns of specialization should be made with caution, particularly when datasets do not account for spatiotemporal variability. Another issue to consider is to evaluate the quality of individual datasets, mainly the possible effects of sampling completeness. Although we demonstrated, similarly to Vizentin-Bugoni et al. (2016), that the quantitative specialization metrics were relatively resistant to sampling completeness, we also showed that the metrics could be largely affected by rare interactions in small networks.

Despite our presentation of more sunbird-plant networks than any previously published study from tropical Africa, our knowledge on sunbird-plant network specialization is still incipient. Furthermore, there is a significant knowledge gap on sunbird food plants. This is illustrated by the fact that the most comprehensive information on food plants in the sunbird monograph by Cheke et al. (2001), which was also used by Fleming and Muchhala (2008) in their evaluation of sunbird specialization, reports only 2 of the 49 food plant species that were visited by sunbirds during our observations on Mt.

Cameroon. Moreover, the idea that forest-dwelling sunbirds, in contrast to hummingbirds, feed more often on canopy and subcanopy trees (Fleming and Muchhala 2008) appears valid only when applied to the dry season. Moreover, it seems that similarly to hummingbirds (Feinsinger 1976), sunbird communities are composed of more assemblages, with some species (such as the Cameroon sunbird, *Cyanomitra oritis*) exploring more specialized flowers in the forest interior, whereas other sunbirds feed on a more generalized variety of canopy trees. Another unexploited but important aspect of sunbird ecology on Mt. Cameroon is the local migration. It seems that in the dry season, at least some individuals of Cameroon sunbirds migrate to lower elevations. Ursula's sunbird disappeared from the mid-altitudinal forest in the wet season, but we did not find it at any other elevation. Thus, because it is an endemic species occurring only in the Cameroonian Highlands and Bioko, we can speculate that it migrates to less rainy Mt. Cameroon slopes. Nevertheless, both the organisation of sunbird assemblages and local migration should be explored by additional studies. This knowledge will be crucial for the effective conservation of Mt. Cameroon's sunbird and plant assemblages.

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Author contribution statement ŠJ originally formulated the ideas. ŠJ, KC, JM, GUG, NTF, MMJ and FLE conducted the fieldwork. Video material was processed by PJ and KC. ŠJ and PJ analysed the data. ŠJ led the writing of the manuscript. All authors contributed critically to the drafts and gave approval for publication.

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Declarations

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References

Abrahamczyk S, Kessler M (2010) Hummingbird diversity, food niche characters, and assemblage composition along a latitudinal precipitation gradient in the Bolivian lowlands. J Ornithol 151:615–625

Adler PB, Fajardo A, Kleinhesselink AR, Kraft NJB (2013) Trait-based tests of coexistence mechanism. Ecol Lett 16:1294–1306

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER:guide to software and statistical methods. PRIMER-E, Plymouth.

Araujo AC, Sazima M (2003) The assemblage of flowers visited by hummingbirds in the "capões" of Southern Pantanal, Mato Grosso do Sul, Brazil. Flora 198:427–435

Bartoš M, Janeček Š (2014) Pollinator-induced twisting of flowers sidesteps floral architecture constraints. Curr Biol 24:R793–R795

Beckett SJ (2016) Improved community detection in weighted bipartite networks. R Soc Open Sci 3:140536

Bentos VT, Mesquita RCG, Williamson GB (2008) Reproductive phenology of Central Amazon pioneer trees. Trop Conserv Sci 1:186–203

Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. BMC Ecol 6:9

Botes C, Johnson SD, Cowling RM (2008) Coexistence of succulent tree aloes: partitioning of bird pollinators by floral traits and flowering phenology. Oikos 117:875–882

Cable S, Cheek M (1998) The plants of Mount Cameroon conservation checklist. Kew: Royal Botanic Gardens, London

Cheke RA, Mann CF, Allen R (2001) Sunbirds: A Guide to the Sunbirds, Flowerpeckers, Spiderhunters and Sugarbirds of the World. Christopher Helm, UK, London

Chmel K, Ewome FL, Gómez GU, Klomberg Y, Mertens JEJ, Tropek R, Janeček Š (2021) Bird pollination syndrome is the plant´s adaptation to ornithophily, but nectarivorous birds are not so selective. Oikos 130:1411–1424

Collins B, Briffa P (1982) Seasonal Variation of Abundance and Foraging of Three Species of Australian Honeyeaters. Wildl Res 9:557–569

Collins BG, Rebelo T (1987) Pollination biology of the Proteaceae in Australia and southern Africa. Austral Ecol 12:387–421

Collins BG (1985) Energetics of foraging and resource selection by honeyeaters in forest and woodland habitats of Western Australia. New Zeal J Zool 12:577–587

Comer SJ, Wooller RD (2002) A comparison of passerine avifaunas of a rehabilitated minesite and a nearby reserve in south-western Australia. Emu 102:305–311

Cronk Q, Ojeda I (2008) Bird-pollinated flowers in an evolutionary and molecular context. J Exp Bot 59:715–727

Cruden RW (1972) Pollinators in high-elevation ecosystems: relative effectiveness of birds and bees. Science 176:1439–1440

Cuartas-Hernández S, Medel R (2015) Topology of plant - flower-visitor networks in a tropical mountain forest: Insights on the role of altitudinal and temporal variation. PLoS ONE 10:e0141804

Dehling DM, Töpfer T, Schaefer HM et al (2014) Functional relationships beyond species richness patterns: trait matching in plant–bird mutualisms across scales. Glob Ecol Biogeogr 23:1085–1093

Dorman CF, Gruber B, Fründ J (2008) Introduction to bipartite package: analysing ecological networks. R News 8:8–11

Dormann CF, Strauss R (2014) A method for detecting modules in quantitative bipartite networks. Methods Ecol Evol 5:90–98

Ebeling A, Klein AM, Tscharntke T (2011) Plant-flower visitor interaction webs: temporal stability and pollinator specialization increases along an experimental plant diversity gradient. Basic Appl Ecol 12:300–309

Feinsinger P (1976) Organization of a tropical guilds of nectarivorous birds. Ecol Monogr 46:257–291

Feinsinger P, Swarm LA, Wolfe JA (1985) Nectar-feeding birds on Trinidad and Tobago: comparison of diverse and depauperate guilds. Ecol Monogr 55:1–28

Ferenc M, Fjeldså J, Sedláček O, Motombi FN, Djomo Nana E, Mudrová K, Hořák D (2016) Abundance-area relationships in bird assemblages along an Afrotropical elevational gradient: space limitation in montane forests selects for higher population densities. Oecologia 181:225–233

Figueroa LL, Grab H, Ng WH, Myers CR, Graystock P, McFrederick QS, McArt SH (2020) Landscape simplification shapes pathogen prevalence in plant-pollinator networks. Ecol Lett 23:1212–1222

Fleming TH, Muchhala N (2008) Nectar-feeding bird and bat niches in two worlds: pantropical comparisons of vertebrate pollination systems. J Biogeogr 35:764–780

Freeman, (1979) Centrality in the social networks I: conceptual clarification. Soc Networks 1:215–239

Geerts S, Pauw A (2009a) African sunbirds hover to pollinate an invasive hummingbird-pollinated plant. Oikos 118:573–579

Geerts S, Pauw A (2009b) Hyper-specialization of long-billed bird pollination in a guild of South African plants: the Malachite Sunbird pollination syndrome. S Afr J Bot 75:699–706

González AMM, Dalsgaard B, Olesen JM (2010) Centrality measures and the importance of generalist species in pollination networks. Ecol Complex 7:36–43

González AMM, Dalsgaard B, Nogués-Bravo D, Graham CH, Schleuning M, Maruyama PK, Abrahamczyk S, Alarcón R, Araujo AC, Araújo FP, de Azevedo Jr SM, BaqueroCotton ACPA, Ingversen TT, Kohler G, Lara C, Las-Casas FMG, Machado AO, Machado CG, Maglianesi MA, McGuire JA, Moura AC, Oliveira GM, Oliveira PE, Ornelas JF, Rodrigues LC, Rosero-Lasprilla L, Rui AM, Sazima M, Timmermann A, Varassin IG, Vizentin-Bugoni J, Wang Z, Watts S, Rahbek C, Martinez ND (2015) The macroecology of phylogenetically structured hummingbird-plant networks. Glob Ecol Biogeogr 24:1212–1224

Hoiss B, Krauss J, Steffan-Dewenter I (2015) Interactive effects of elevation, species richness, and extreme climatic events on plant pollinator networks. Glob Change Biol 21:4086–4097

Hořák D, Ferenc M, Sedláček O, Motombi FN, Svoboda M, Altman J, Albrecht T, Nana ED, Janeček Š, Dančak M, Majeský L, Lltonga EN, Doležal J (2019) Forest structure determines spatial changes in avian communities along an elevational gradient in tropical Africa. J Biogeogr 46:2466–2478

Huang ZH, Song YP, Huang SQ (2017) Evidence for passerine bird pollination in *Rhododendron* species. AoB Plants 9:0plx062

Infante SD, Lara C, Arizmendi MC (2020) Temporal dynamics of the hummingbird-plant interaction network of a dry forest in Chamela, Mexico: a 30-year follow-up after two hurricanes. PeerJ 8:e8338. https://doi.org/10.7717/peerj.8338

Jacobi CM, Antonini Y (2008) Pollinators and defence of *Stachytarpheta glabra* (Verbenaceae) nectar resources by the hummingbird *Colibri serrirostris* (Trochilidae) on ironstone outcrops in south–east Brazil. J Trop Ecol 24:301–308

Janeček Š, Patáčová E, Bartoš M, Padyšáková E, Spitzer L, Tropek R (2011) Hovering sunbirds in the Old World: occasional behaviour or evolutionary trend? Oikos 120:178–183

Janeček Š, Riegert J, Sedláček O, Bartoš M, Hořák D, Reif J, Padyšáková E, Fainová D, Antczak M, Pešata M, Mikeš V, Patáčová E, Altman J, Kantorová J, Hrázský Z, Brom J, Doležal J (2012) Food selection by avian floral visitors: an important aspect of plant-flower visitor interactions in West Africa. Biol J Linnean Soc 107:355–367

Janeček Š, Bartoš M, Njabo KY (2015) Convergent evolution of sunbird pollination systems of Impatiens species in tropical Africa and hummingbird systems of the New World. Biol J Linnean Soc 115:127–133

Janeček Š, Chmel K, Ewome FL, Hrubá K, Klomberg Y, Kobe IN, Kouede RD, Mertens JEJ, Njie MM, Tropek R (2021) Differences in nectar traits between ornithophilous and entomophilous plants on Mount Cameroon. Plants 10:1161

Janečková P, Sejfová Z, Janeček Š, Chmel K, Chmelová E, Ewome FL (2021) Behavioural correlates of drinking speed in two West African sunbird species. Bird Study 67:540–542

Janzen DH (1967) Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21:620–637

Klomberg Y, Tropek R, Mertens JEJ, Kobe IN, Hodeček J, Raška J, Fominka NT, Souto-Vilarós D, Janečková P, Janeček Š (2022) Spatiotemporal variation in the role of floral traits in shaping tropical plant-pollinator interactions. Ecol Lett 25:839–850

Küper W, Sommer JH, Lovett JC, Beentje HJ, van Rompaey RSAR, Chatelain C, Sosef M, Barthlott W (2004) Africa's hotspots of biodiversity redefined. Ann Mo Bot Gard 91:525–535

Linder HP (2014) The evolution of African plant diversity. Front Ecol Evol 2:38

Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M (2014) Morphological traits determine specialization and resource use in plant–hummingbird networks in the neotropics. Ecology 95:3325–3334

Maglianesi MA, Blüthgen N, Böhning-Gaese K, Schleuning M (2015) Functional structure and specialization in three tropical plant-hummingbird interaction networks across an elevational gradient in Costa Rica. Ecography 38:1119–1128

Maicher V, Sáfián S, Murkwe M, Delabye S, Przybyłowicz Ł, Potocký P, Kobe IN, Janeček Š, Mertens JEJ, Fokam EB, Pyrcz T, Doležal J, Altman J, Hořák D, Fiedler K, Tropek R (2020) Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. J Biogeogr 47:342–354

Maruyama PK, Sonne J, Bugoni JV, González AMM, Zanata TB, Abrahamczyk S, Alarcón R, Araujo AC, Araújo FP, Baquero AC, Chávez-González E, Coelho AG, Cotton PA, Dehling DM, Fischer E, Kohler G, Lara C, Las-Casas FMG, Machado AO, Machado CG, Maglianesi MA, Malucelli TS, Marín-Gómez OH, Oliveira PE, Ornelas JF, Ortiz-Pulido R, Ramírez-Burbano MB, Rocca MA, Rodrigues LC, Rosero-Lasprilla L, Rui AM, Sandel B, Svenning JC, Tinoco BA, Varassin IG, Watts S, Rahbek C, Sazima M, Schleuning M, Dalsgaard B (2018) Functional diversity mediates macroecological variation in plant–hummingbird interaction networks. Glob Ecol Biogeogr 27:1186–1199

Maruyama PK, Vizentin-Bugoni J, Oliveira GM, Oliveira PE, Dalsgaard B (2014) Morphological and spatio-temporal mismatches shape a neotropical savanna plant-hummingbird network. Biotropica 46:740–747

MacArthur RH (1968) The theory of the niche. In: Lewontin RC (ed) Population biology and evolution. Syracuse Univ. Press, Syracuse, N.Y., pp 159–176

Miller-Struttmann NE, Galen C (2014) High-altitude multi-taskers: bumble bee food plant broadens along an altitudinal productivity gradient. Oecologia 176:1033–1045

Newman MEJ (2004) Fast algorithm for detecting community structure in networks. Phys Rev E 69

Newman MEJ (2006) Modularity and community structure in networks. Proc Natl Acad Sci 103:8577–8582

Nsor CA, Godsoe W, Chapman HM (2019) Promiscuous pollinators—evidence of an Afromontane sunbird–plant pollen transport network. Biotropica 51:538–548

Ollerton J, Cranmer L (2002) Latitudinal trends in plant-pollinator interactions: are tropical plants more specialised? Oikos 98:340–350

Ollerton J (2012) Biogeography: are tropical species less specialised? Curr Biol 22:R914–R915

Ollerton J, Nuttman C (2013) Aggressive displacement of carpenter bees *Xylocopa nigrita* from flowers of *Lagenaria sphaerica* (Cucurbitaceae) by territorial male eastern olive sunbirds (*Cyanomitra olivacea*) in Tanzania. J Pollinat Ecol 11:21–26

Partida-Lara R, Enríquez PL, Vázquez-Pérez JR, de Bonilla EPD, Martínez-Ico M, Rangel-Salazar JL (2018) Pollination syndromes and interaction networks in hummingbird assemblages in El Triunfo Biosphere Reserve, Chiapas, Mexico. J Trop Ecol 34:293–307

Pellissier L, Albouy C, Bascompte J, Farwig N, Graham C, Loreau M, Maglianesi MA, Melián CJ, Pitteloud C, Roslin T, Rohr R, Saavedra S, Thuiller W, Woodward G, Zimmermann NE, Gravel D (2017) Comparing species interaction networks along environmental gradients. Biol Rev 93:785–800

Paton DC, Collins BG (1989) Bills and tongues of nectar-feeding birds: a review of morphology, function and performance, with intercontinental comparison. Aust J Ecol 14:473–506

Quintero E, Genzoni E, Mann N, Nuttman C, Anderson B (2017) Sunbird surprise: a test of the predictive power of the syndrome concept. Flora 232:22–29

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ramírez SR, Eltz T, Fujiwara MK, Gerlach G, Goldman-Huertas B, Tsutsui ND, Pierce NE (2011) Asynchronous diversification in a specialized plant-pollinator mutualism. Science 333:1742–1746

Ramos-Jiliberto R, Domínguez D, Espinoza C, López G, Valdovinos FS, Bustamante RO, Medel R (2010) Topological change of Andean plant–pollinator networks along an altitudinal gradient. Ecol Complex 7:86–90

Rasmann S, Alvarez N, Pellissier L (2014) The altitudinal niche-hypothesis in insect-plant interactions. Annu Plant Rev 47:339–360

Rebelo AG (1987) Bird pollination in the Cape Flora. In: Rebelo AG (ed) A preliminary synthesis of pollination biology in the Cape flora. S. Afr. nat. Sci. Prog. Rep. 141. CSlR, Pretoria, SA, pp 83–108

Schmid B, Nottebrock H, Esler KJ, Pagel J, Pauw A, Böhning-Gaese K, Schurr FM, Schleuning M (2016) Responses of nectar-feeding birds to floral resources at multiple spatial scales. Ecography 39:619–629

Sejfová Z, Mlíkovský J, Ewome FL, Janečková P, Klomberg Y, Njie MM, Janeček Š (2021) Sunbirds' tendency to hover: the roles of energetic rewards, inflorescence architecture and rain. J Avian Biol 52:e02818

Simmons BI, Vizentin-Bugoni J, Maruyama PK, Cotton PA, Marín-Gómez OH, Lara C, Rosero-Lasprilla L, Maglianesi MA, Ortiz-Pulido R, Rocca MA, Rodrigues LC, Tinoco BA, Vasconcelos MF, Sazima M, González AMM, Sonne J, Rahbek C, Dicks LV, Dalsgaard B, Sutherland WJ (2019) Abundance drives broad patterns of generalisation in plant–hummingbird pollination networks. Oikos 128:1287–1295

Snow BK, Snow DW (1972) Feeding niches of hummingbirds in Trinidad valley. J Anim Ecol 41:471–485

Sonne J, Zanata TB, González AMM, Torres NLC, Fjeldså J, Colwell RK, Tinoco BA, Rahbek C, Dalsgaard B (2019) The distributions of morphologically specialized hummingbirds coincide with floral trait matching across an Andean elevational gradient. Biotropica 51:205–218

Souza CS, Maruyama PK, Aoki C, Sigrist MR, Raizer J, Gross CL, de Araujo AC (2018) Temporal variation in plant-pollinator networks from seasonal tropical environments: higher specialization when resources are scarce. J Ecol 106:2409–2420

Stiles FG (1981) Geographical aspects of bird-flower coevolution, with particular reference to Central America. Ann Mo Bot Gard 68:323–351

Tinoco BA, Graham CH, Aguilar JM, Schleuning M (2017) Effects of hummingbird morphology on specialization in pollination networks vary with resource availability. Oikos 126:52–60

Tropek R, Bartoš M, Padyšáková E, Janeček Š (2013) Interference competition between sunbirds and carpenter bees for the nectar of *Hypoestes aristata*. Afr Zool 48:392–394

Vanbergen AJ, Woodcock BA, Heard MS, Chapman DS (2017) Network size, structure and mutualism dependence affect the propensity for plant-pollinator extinction cascades. Funct Ecol 31:1285–1293

Vázquez DP, Melián CJ, Williams NM, Blüthgen N, Krasnov BR, Poulin R (2007) Species abundance and asymmetric interaction strength in ecological networks. Oikos 116:1120–1127

Vizentin-Bugoni J, Maruyama PK, Debastiani VJ, Duarte LDS, Dalsgaard B, Sazima M (2016) Influences of sampling effort on detected patterns and structuring processes of a Neotropical plant-hummingbird network. J Anim Ecol 85:262–272

Weinstein BG (2015) Motion Meerkat: integrating motion video detection and ecological monitoring. Methods Ecol Evol 6:357–362

Wester P (2014) Feeding on the wing: hovering in nectar-drinking Old World birds-more common than expected. Emu 114:171–183

Wester P (2013) Sunbirds hover at flowers of *Salvia* and *Lycium*. Ostrich 84:27–32

Wolf LL (1970) The impact of seasonal flowering on the biology of some tropical hummingbirds. The Condor 72:1–14

Zanata TB, Dalsgaard B, Passos FC, Cotton PA, Roper JJ, Maruyama PK, Fischer E, Schleuning M, González AMM, Vizentin-Bugoni J, Franklin DC, Abrahamczyk S, Alárcon R, Araujo AC, Araújo FP, de Azevedo Jr SM, Baquero AC, Böhning-Gaese K, Carstensen DW, Chupil H, Coelho AG, Faria RR, Hořák D, Ingversen TT, Janeček Š, Kohler G, Lara C, Las-Casas FMG, Lopes AV, Machado AO, Machado CG, Machado IC, Maglianesi MA, Malucelli TS, Mohd-Azlan J, Moura AC, Oliveira GM, Oliveira PE, Ornelas JF, Riegert J, Rodrigues LC, Rosero-Lasprilla L, Rui AM, Sazima M, Schmid B, Sedláček O, Timmermann A, Vollstädt MGR, Wang Z, Watts S, Rahbek C, Varassin IG (2017) Global patterns of interaction specialization in bird-flower networks. J Biogeogr 44:1891–1910

SUPPORTING INFORMATION CHAPTER 6

Janeček, Š., Chmel, K., Mlíkovský, J., **Uceda-Gomez, G.**, Janečková, P., Fominka, N.T., Njie, M.M., & Ewome, F.L. (2022). Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. *Oecologia*, 199, 885-896. https://doi.org/10.1007/s00442-022-05234-4

The interaction frequencies for each of the eight networks (i.e., Supplementary file 2) can be found at:

https://link.springer.com/article/10.1007/s00442-022-05234-4#Sec12

Table S1: Observation effort for individual plant species and plant density

Camp	Season	Observation	Species	Observation time (hrs.)	Number of flowering plants per hectare
MANN'S SPRING	dry	camera	*Acanthopale decempedalis*	216.8	22.5
MANN'S SPRING	dry	camera	*Hypoestes triflora*	223.5	30
MANN'S SPRING	dry	camera	*Impatiens sakeriana*	218.6	1.67
MANN'S SPRING	dry	camera	*Isoglossa glandulifera*	198.4	6.67
MANN'S SPRING	wet	camera	*Acanthopale decempedalis*	211.3	6.67
MANN'S SPRING	wet	camera	*Chassalia laikomensis*	207.9	6.67
MANN'S SPRING	wet	camera	*Disperis kamerunensis*	182.3	2.5
MANN'S SPRING	wet	camera	*Impatiens sakeriana*	160.9	1.67
MANN'S SPRING	wet	camera	*Isoglossa glandulifera*	109.8	0.83
MANN'S SPRING	wet	camera	*Jasminum preussii*	202.4	5
MANN'S SPRING	wet	camera	*Liparis sp.*	167.1	0.5
MANN'S SPRING	wet	camera	*Psychotria hypsophila*	251.5	74.17
MANN'S SPRING	wet	camera	*Rhipidoglossum sp.*	167.2	2.5
CRATER LAKE	dry	camera	*Acanthopale decempedalis*	226.3	9.17
CRATER LAKE	dry	camera	*Aframomum sp. purple*	220.5	3.33
CRATER LAKE	dry	camera	*Aframomum sp. white*	210.4	5.83
CRATER LAKE	dry	camera	*Brillantaisia owariensis*	222.9	2.5
CRATER LAKE	dry	camera	*Costus dubius*	170.6	0.5
CRATER LAKE	dry	camera	*Hypoestes triflora*	235.1	93.3
CRATER LAKE	dry	camera	*Impatiens burtonii*	258.4	1.67
CRATER LAKE	dry	camera	*Impatiens niamniamensis*	212.1	0.83
CRATER LAKE	dry	camera	*Isoglossa glandulifera*	203.1	1.67
CRATER LAKE	dry	camera	*Ixora guineensis*	24	5
CRATER LAKE	dry	camera	*Mimulopsis solmsii*	225.1	5
CRATER LAKE	dry	camera	*Plectranthus kamerunensis*	219.8	3.33
CRATER LAKE	dry	camera	*Stachys aculeolata*	115	0.5
CRATER LAKE	dry	camera	*Thonningia sanguinea*	93.5	0.5
CRATER LAKE	wet	camera	*Acanthopale decempedalis*	242.8	4.17
CRATER LAKE	wet	camera	*Aframomum sp. purple*	90.1	0.5
CRATER LAKE	wet	camera	*Aframomum sp. white*	106.9	0.83
CRATER LAKE	wet	camera	*Calanthe sylvatica*	80.4	1.67
CRATER LAKE	wet	camera	*Chassalia laikomensis*	180	4.17
CRATER LAKE	wet	camera	*Clerodendrum sylvanum*	246	2.5
CRATER LAKE	wet	camera	*Costus dubius*	135.1	0.5
CRATER LAKE	wet	camera	*Cynorkis ringens*	44	0.5

CRATER LAKE	wet	camera	*Disperis nitida*	112.1	1.67
CRATER LAKE	wet	camera	*Impatiens burtonii*	111.1	15.83
CRATER LAKE	wet	camera	*Impatiens etindensis*	232.8	6.67
CRATER LAKE	wet	camera	*Impatiens niamniamensis*	238.5	5.83
CRATER LAKE	wet	camera	*Ixora guineensis*	138	10
CRATER LAKE	wet	camera	*Plectranthus kamerunensis*	88.8	6.67
CRATER LAKE	wet	camera	*Rhipidoglossom sp.*	88.9	0.83
CRATER LAKE	wet	camera	*Stachys aculeolata*	120.5	24.17
CRATER LAKE	wet	camera	*Thonningia sanguinea*	230.6	17.5
CRATER LAKE	wet	camera	*Urticularia manniii*	115.7	22.5
PLANTECAM CAMP	dry	camera	*Aframomum sp1*	217.6	9.17
PLANTECAM CAMP	dry	camera	*Brillantaisia owariensis*	224.5	1.67
PLANTECAM CAMP	dry	camera	*Calochone acuminata*	108.4	0.5
PLANTECAM CAMP	dry	camera	*Costus dubius*	205.6	0.83
PLANTECAM CAMP	dry	camera	*Dischistocalyx grandiflora*	223.2	3.33
PLANTECAM CAMP	dry	camera	*Impatiens niamniamensis*	240.4	0.83
PLANTECAM CAMP	dry	camera	*Pavetta rigida*	132.6	1.67
PLANTECAM CAMP	dry	camera	*Sabicea pilosa*	215.3	1.67
PLANTECAM CAMP	dry	camera	*Scadoxus cinnabarinus*	180.3	1.67
PLANTECAM CAMP	dry	camera	*Schumanniophyton magnificum*	64.4	0.5
PLANTECAM CAMP	dry	camera	*Sherbournia bignoniiflora*	134.9	0.5
PLANTECAM CAMP	wet	camera	*Acanthonema strigosum*	90.3	11.67
PLANTECAM CAMP	wet	camera	*Calanthe sylvestris*	112.7	2.5
PLANTECAM CAMP	wet	camera	*Costus dubius*	117.8	0.83
PLANTECAM CAMP	wet	camera	*Impatiens etindensis*	91.2	0.5
PLANTECAM CAMP	wet	camera	*Impatiens frithii*	153.3	6.67
PLANTECAM CAMP	wet	camera	*Impatiens hians*	124.3	0.83
PLANTECAM CAMP	wet	camera	*Impatiens mannii*	44.9	13.33
PLANTECAM CAMP	wet	camera	*Impatiens niamniamensis*	121.8	12.5
PLANTECAM CAMP	wet	camera	*Leea guineensis*	13	0.5
PLANTECAM CAMP	wet	camera	*Plectranthus decurrens*	53.4	3.33
PLANTECAM CAMP	wet	camera	*Psychotria thonneri*	104.3	7.5
PLANTECAM CAMP	wet	camera	*Thonningia sanguinea*	123.7	5
PLANTECAM CAMP	wet	camera	*Thunbergia fasciculata*	107.4	3.33
DRINK GARI	dry	camera	*Acanthonema strigosum*	227	28.33
DRINK GARI	dry	camera	*Aframomum sp.*	218.7	14.17
DRINK GARI	dry	camera	*Dischistocalyx grandiflora*	234.6	12.5
DRINK GARI	dry	camera	*Impatiens niamniamensis*	237.3	5.83
DRINK GARI	dry	camera	*Ixora guineensis*	241.9	61.67
DRINK GARI	dry	camera	*Pavetta neurocarpa*	11.5	0.5
DRINK GARI	dry	camera	*Sabicea calycina*	226.8	6.67

DRINK GARI	dry	camera	*Sabicea pilosa*	229.3	11.67
DRINK GARI	dry	camera	*Voacanga bracteosa*	208.3	3.33
DRINK GARI	wet	camera	*Acanthonema strigosum*	95.9	94.17
DRINK GARI	wet	camera	*Aframomum sp1*	40.5	0.83
DRINK GARI	wet	camera	*Bertiera racemosa*	70.6	0.5
DRINK GARI	wet	camera	*Clerodendrum sylvanum*	118.1	30.83
DRINK GARI	wet	camera	*Dischistocalyx grandiflora*	106.2	26.67
DRINK GARI	wet	camera	*Impatiens niamniamensis*	124.7	19.17
DRINK GARI	wet	camera	*Impatiens hians*	110.1	4.17
DRINK GARI	wet	camera	*Impatiens macroptera*	134.6	80.83
DRINK GARI	wet	camera	*Justicia laxa*	105.1	25.83
DRINK GARI	wet	camera	*Leea guineensis*	55.6	2.5
DRINK GARI	wet	camera	*Marantochloa monophyla*	41.2	6.67
DRINK GARI	wet	camera	*Plectranthus decurrens*	109	8.33
DRINK GARI	wet	camera	*Psychotria thonneri*	55.8	32.5
MANN'S SPRING	dry	personal	*Clausena anisata*	64	0.5
MANN'S SPRING	dry	personal	*Ixora foliosa*	68	9.17
MANN'S SPRING	dry	personal	*Nuxia congesta*	64.1	2.5
MANN'S SPRING	dry	personal	*Psydrax dunlapii*	64	9.17
MANN'S SPRING	dry	personal	*Shefflera abyssinica*	65.1	0.83
MANN'S SPRING	dry	personal	*Syzygium staudtii*	64	6.67
CRATER LAKE	dry	personal	*Dicranolepis vestita*	64	107.5
CRATER LAKE	dry	personal	*Englerina gabonensis*	64	2.5
CRATER LAKE	dry	personal	*Kigelia africana*	64	5.83
CRATER LAKE	dry	personal	*Mussaenda tenuiflora*	64	0.5
CRATER LAKE	dry	personal	*Psydrax dunlapii*	64	5.83
CRATER LAKE	dry	personal	*Syzygium sp.*	64	5.83
CRATER LAKE	dry	personal	*Tabernaemontana ventricosa*	64	62.5
CRATER LAKE	wet	personal	*Anthocleista scandens*	64	5
CRATER LAKE	wet	personal	*Mussaenda tenuiflora*	62	0.5
PLANTECAM CAMP	dry	personal	*Anthonotha fragrans*	44	5.83
PLANTECAM CAMP	dry	personal	*Cordia aurantiaca*	16	0.5
PLANTECAM CAMP	dry	personal	*Kigelia africana*	60.2	8.33
PLANTECAM CAMP	dry	personal	*Mussaenda tenuiflora*	119.6	0.5
PLANTECAM CAMP	dry	personal	*Tabernaemontana ventricosa*	70	11.67
PLANTECAM CAMP	dry	personal	*Voacanga africana*	64	8.33
PLANTECAM CAMP	wet	personal	*Mussaenda tenuiflora*	71.6	0.5
DRINK GARI	dry	personal	*Anthonotha fragrans*	74.3	1.67
DRINK GARI	dry	camera	*Berlinia bracteosa*	64	4.17
DRINK GARI	dry	personal	*Heinsia crinita*	32	2.5

DRINK GARI	dry	personal	*Hugonia micans*	48	0.5
DRINK GARI	dry	personal	*Psilanthus mannii*	47.9	0.5
DRINK GARI	dry	personal	*Tabernaemontana brachyantha*	62	10.83
DRINK GARI	wet	personal	*Phragmanthera kamerunensis*	77.2	0.83

Table S2: Effect of season and forest type on bird and plant specialization, expressed as Blüthgen´s specialization index (d’) and normalized degree (ND). Permutation ANOVA. * 0.01<p<0.05; **p<0.01
The analyses are the same as those in Table 1 in the main text of the manuscript, but the interaction strengths in the networks were not considered per hectare. In other words, interaction strengths were just visits/h on one individual of a particular plant species.

	Bird d´		**Bird ND**		**Plant d´**		**Plant ND**	
	$F_{ps.}$	$p_{perm.}$	$F_{ps.}$	$p_{perm.}$	$F_{ps.}$	p_{perm}	$F_{ps.}$	p_{perm}
Season	1.22	0.263	0.19	0.667	0.55	0.470	0.50	0.487
Forest	4.69	0.013*	5.27	0.004**	6.75	0.001**	12.72	0.001**
Forest*season	0.92	0.426	0.14	0.926	0.38	0.78	0.32	0.790

Table S3. Network-level specialization indices and their differences from the null models (Δ values**)** for networks in individual forest types and seasons. H2´ – network specialization index; Q – modularity; C – connectance. Observed values marked by asterisks differ from the null model prediction: * 0.01<p<0.05; **p<0.01. The analyses are the same as those in Table 2 in the main text of the manuscript, but the interaction strengths in the networks were not considered per hectare. In other words, interaction strengths were just visits/h on one individual of a particular plant species.

	Lowland forest		**Mid-elevation forest**		**Submontane forest**		**Mountain forest**	
	dry	**wet**	**dry**	**wet**	**dry**	**wet**	**dry**	**wet**
H2´$_{OBS}$	0.21**	0.41	0.20**	0.51**	0.57**	0.45**	0.06**	0.19*
Δ H2´	0.13	0.16	0.18	0.39	0.55	0.38	0.06	0.12
Q$_{OBS}$	0.19**	0.24*	0.14**	0.37**	0.30**	0.21**	0.02**	0.04**
ΔQ	0.14	0.15	0.13	0.29	0.29	0.17	0.02	0.02
C	0.33	0.37	0.45	0.44	0.78	0.71	0.89	0.75

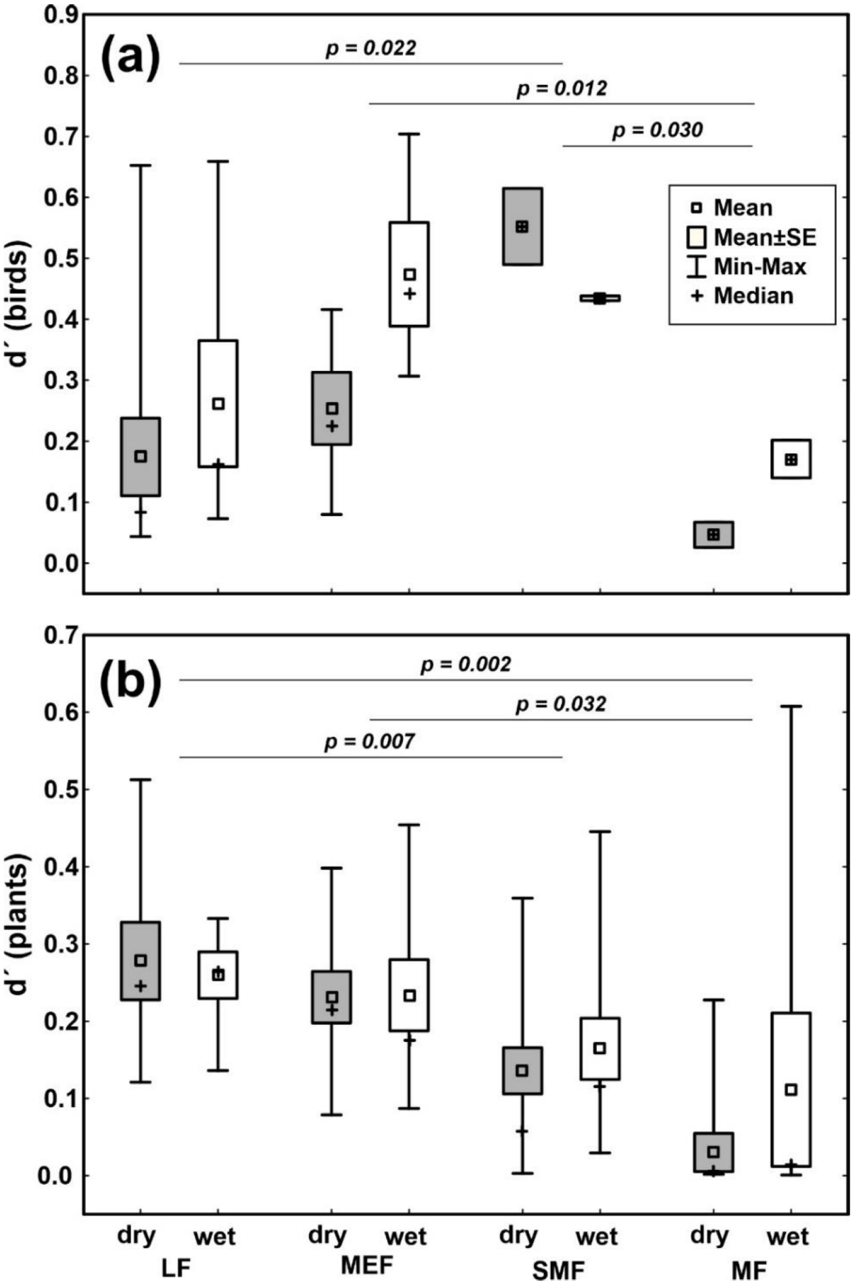

Figure S1. Specialization of birds (a) and plants (b) in different forest types on Mt. Cameroon. d' – Blüthgen´s specialization index; ND – normalized degree. d' was calculated from networks where the interaction strength was expressed as a number of visits h^{-1} per plant. Significant pairwise differences between individual forest types are reported. LF – lowland forest; MEF – mid-elevation forest; SF – submontane forest; MF –montane forest.

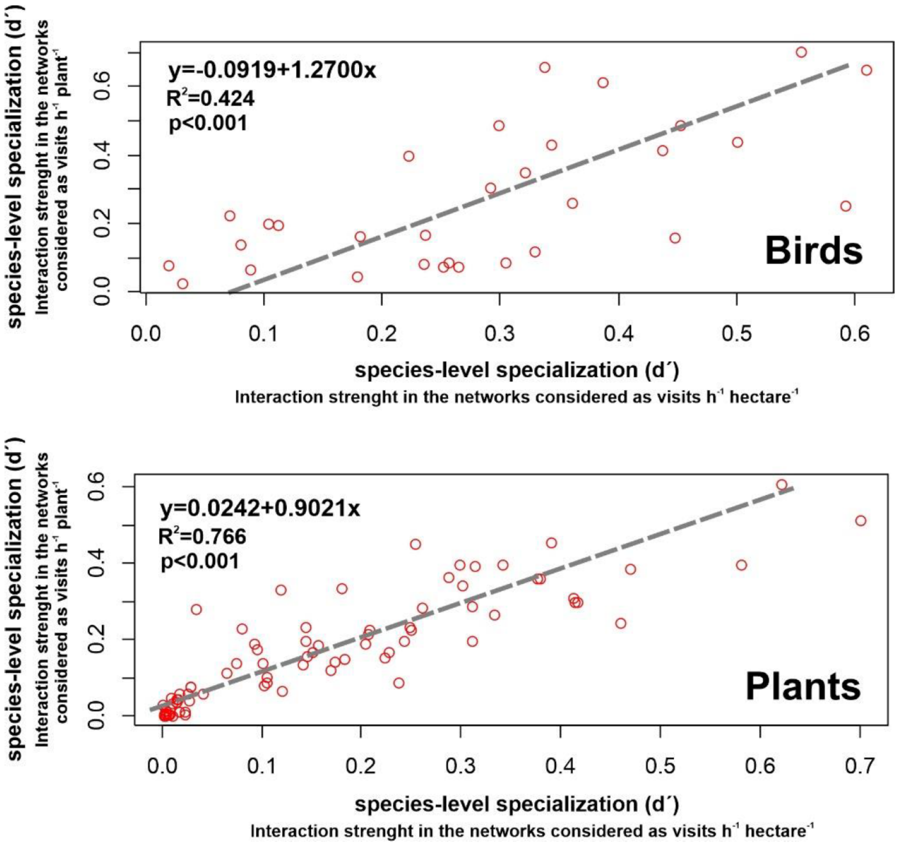

Figure S2. Correlation between species-level specialization indices (d') calculated from networks where the interaction strength was expressed as a number of visits h^{-1} per plant (y-axis) and as a number of visits per hectare (x-axis). Points represent the individual species of birds (upper graph) and plants (bottom graph) from all networks. The grey lines are the standardised major axis estimations (for more details, see Warton D, Duursma R, Falster D, Taskinen S. 2012. SMATR 3 – an R package for estimation and inference about allometric lines. Methods in Ecology and Evolution 3: 257–259.)

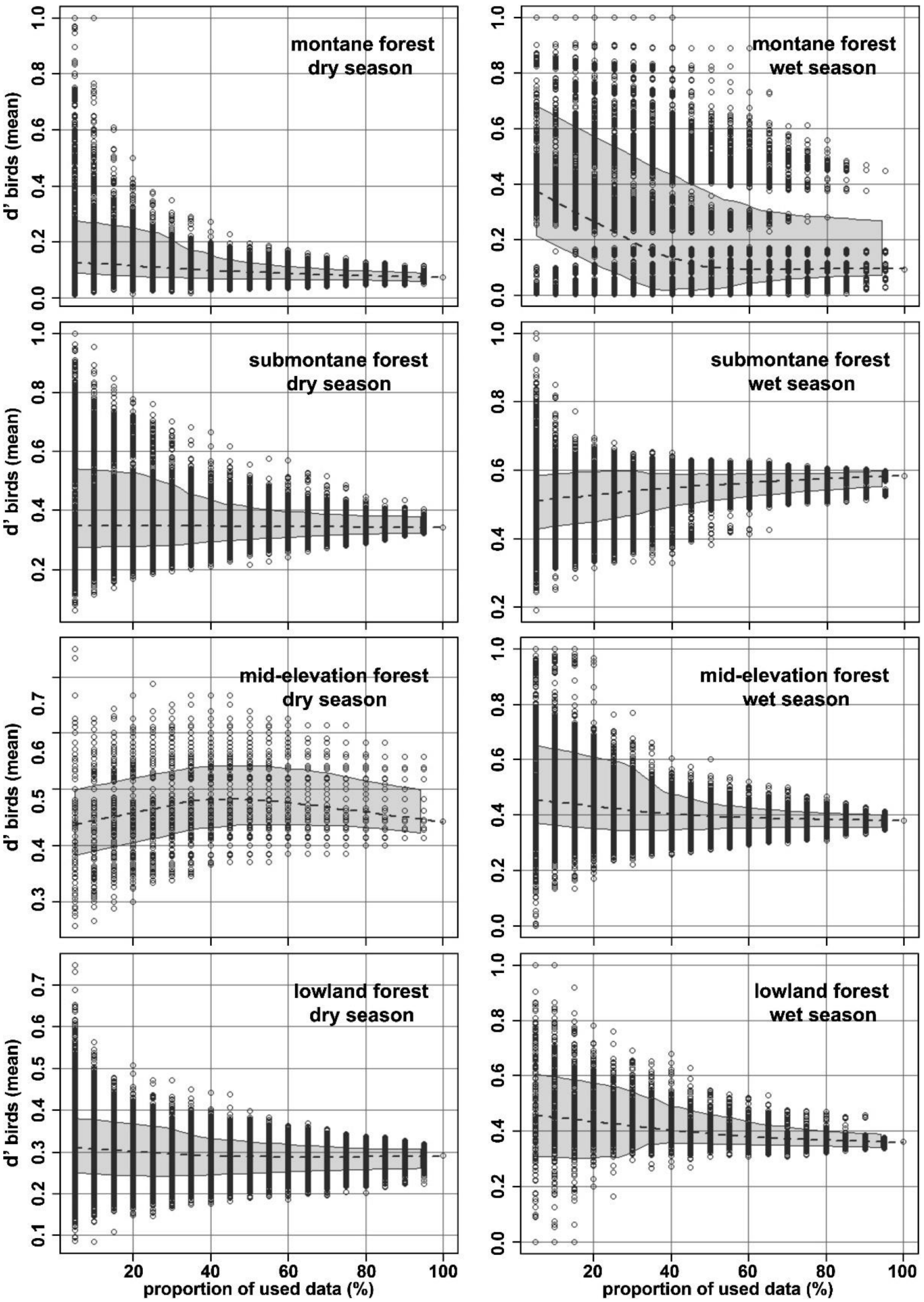

Figure S3. Effects of sampling effort on species level specialization of sunbirds measured by Blüthgen's d'. The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

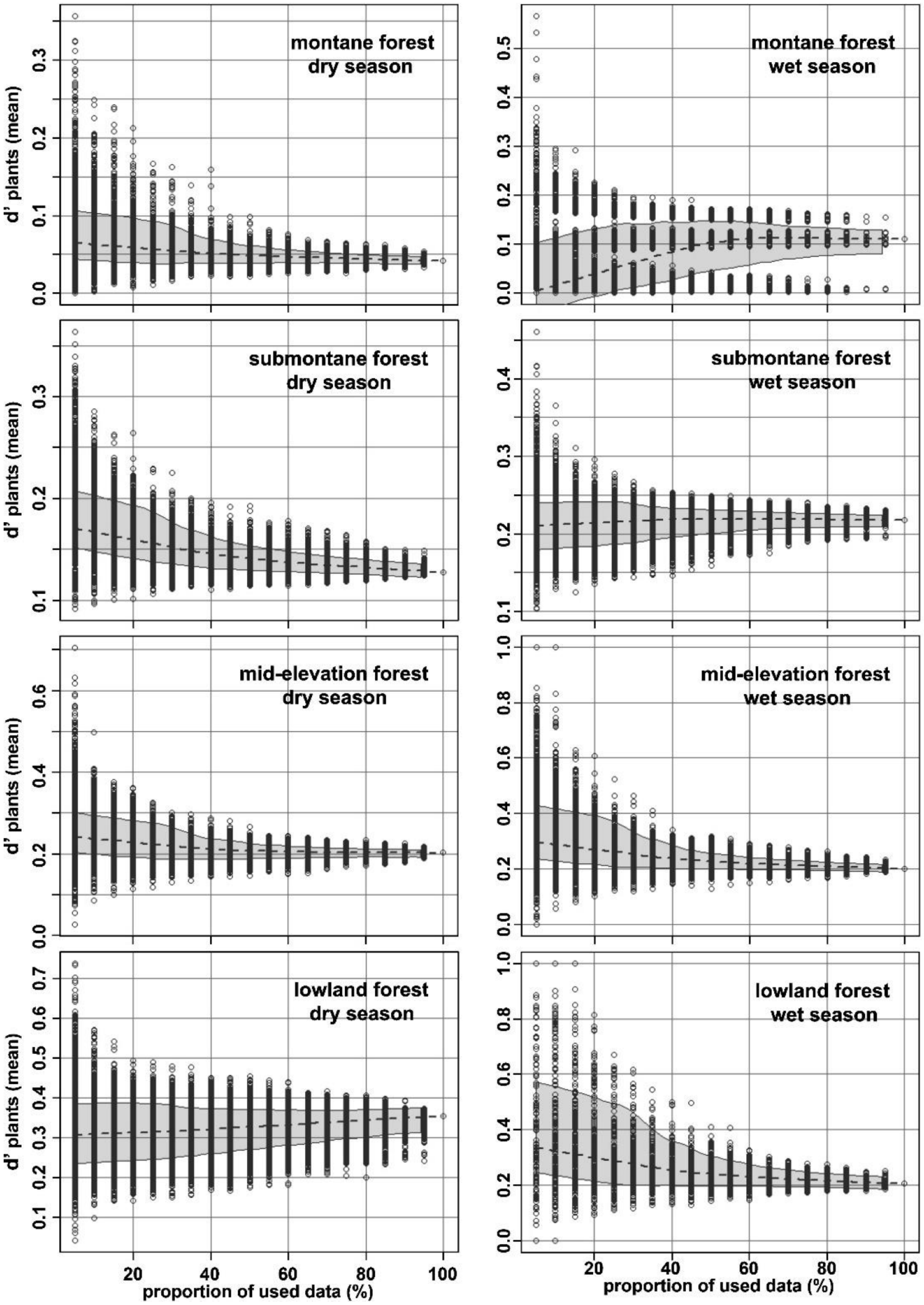

Figure S4. Effects of sampling effort on species level specialization of plants measured by Blüthgen's d'. The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

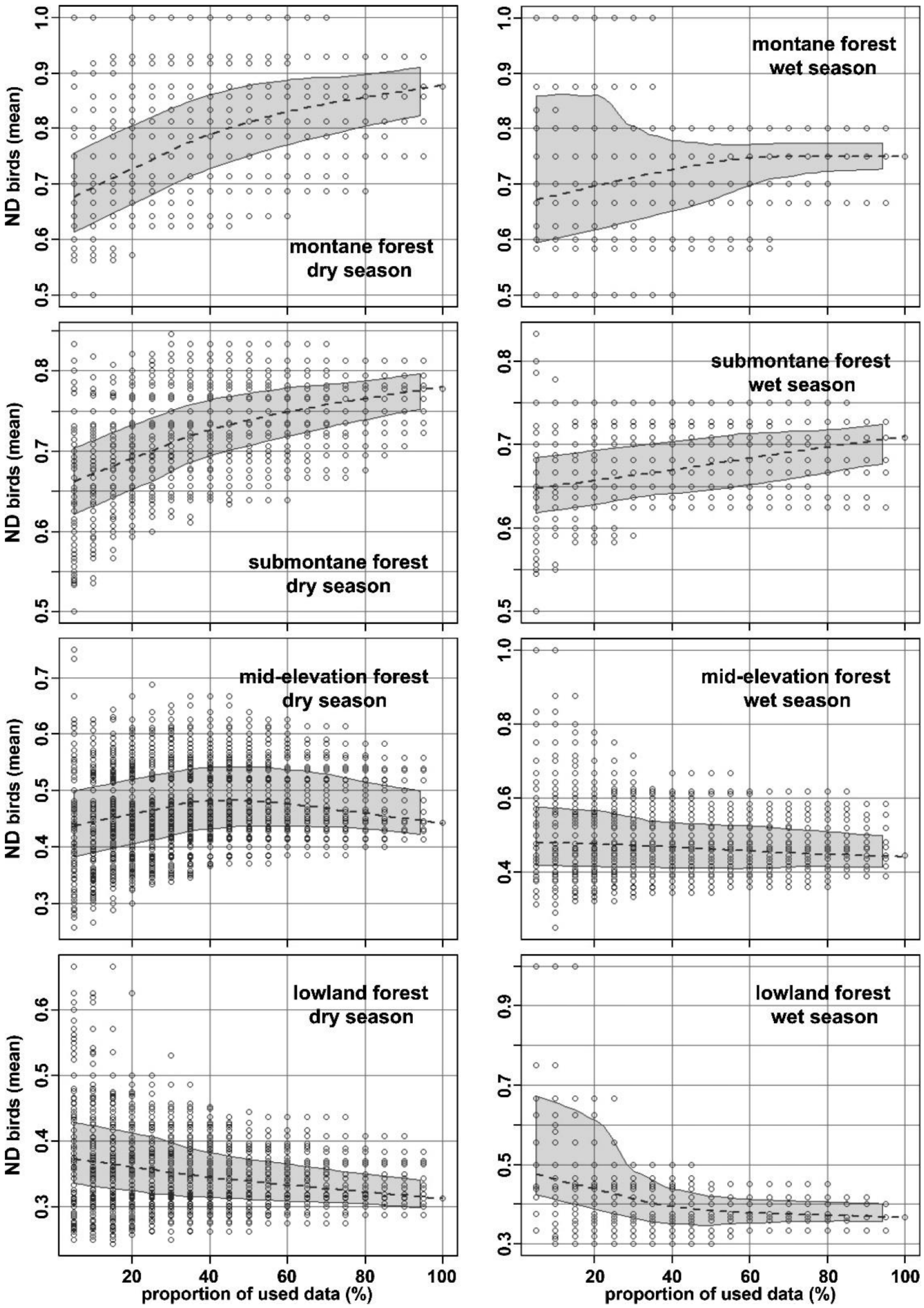

Figure S5. Effects of sampling effort on species level specialization of sunbirds measured by normalized degree (ND). The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

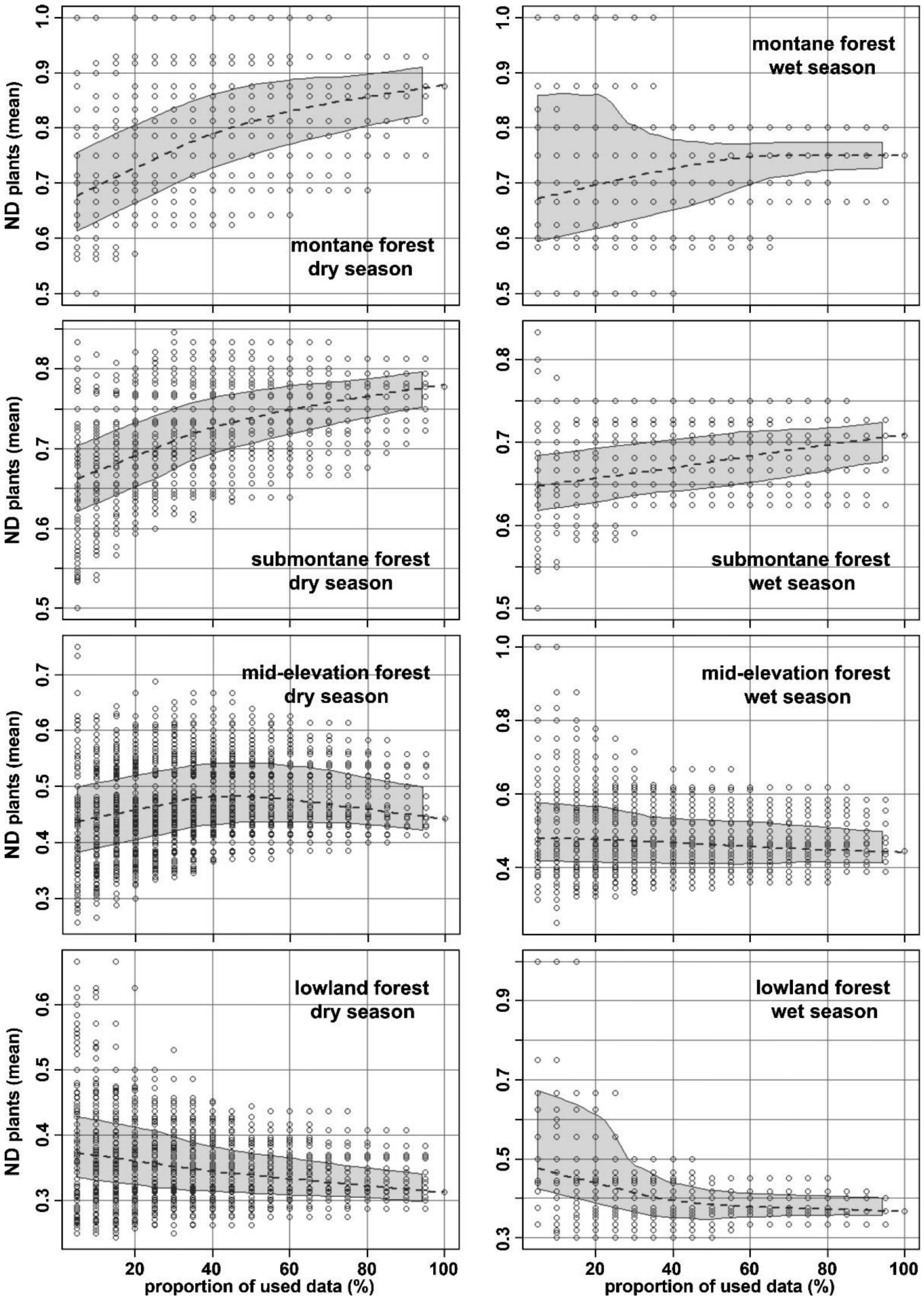

Figure S6. Effects of sampling effort on species level specialization of plants measured by normalized degree (ND). The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

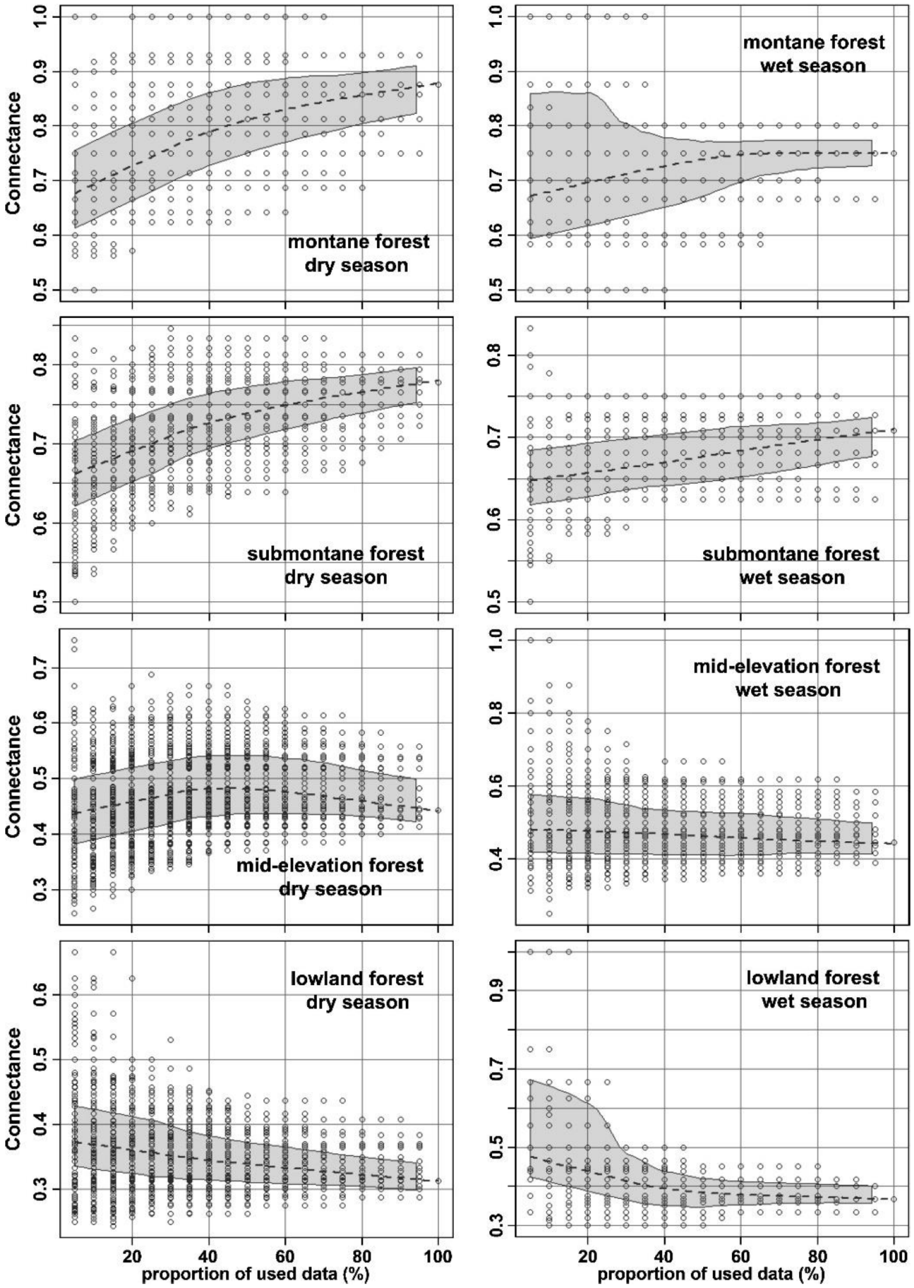

Figure S7. Effects of sampling effort on network connectance. The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

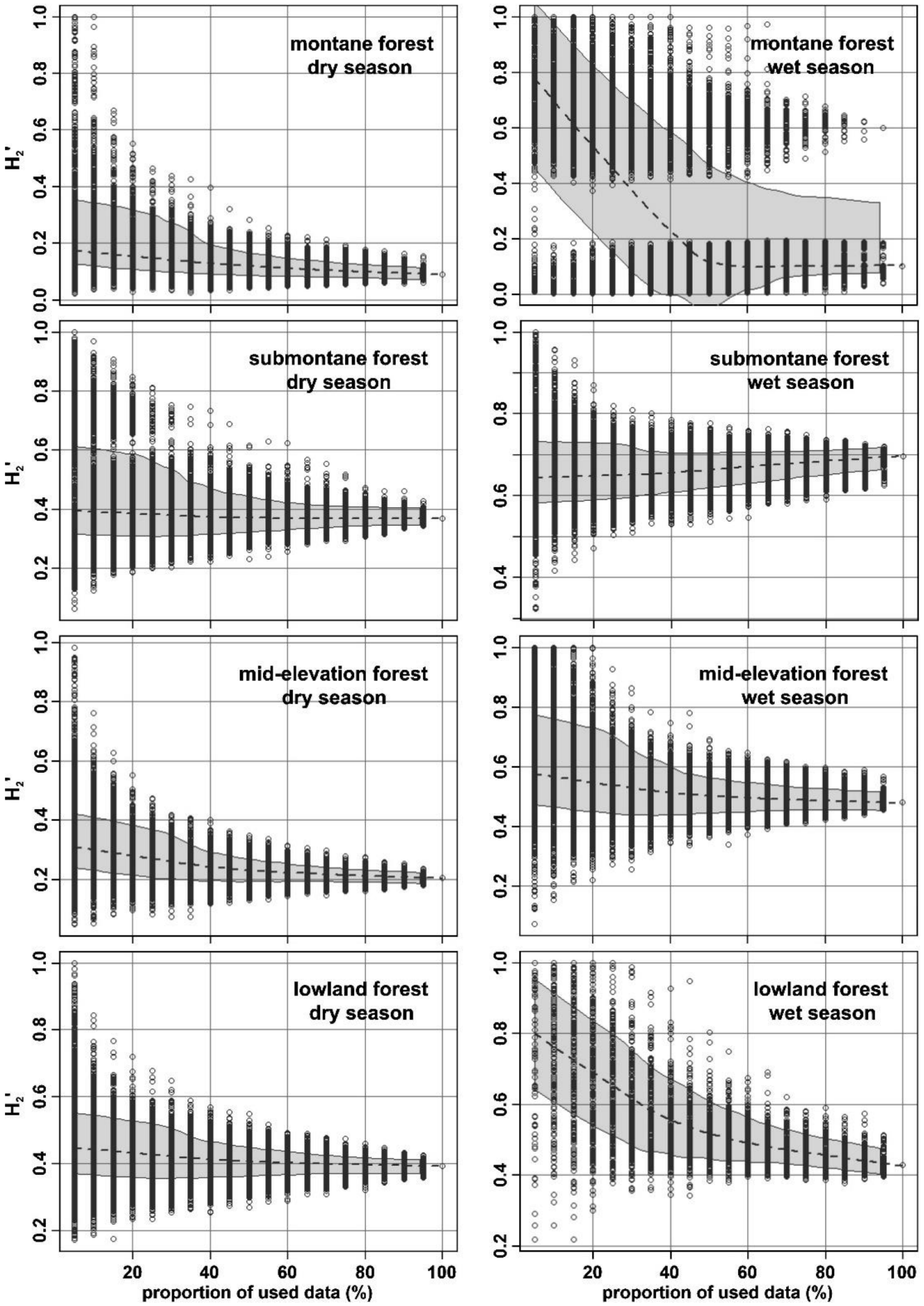

Figure S8. Effects of sampling effort on network complementary specialization (H_2'). The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

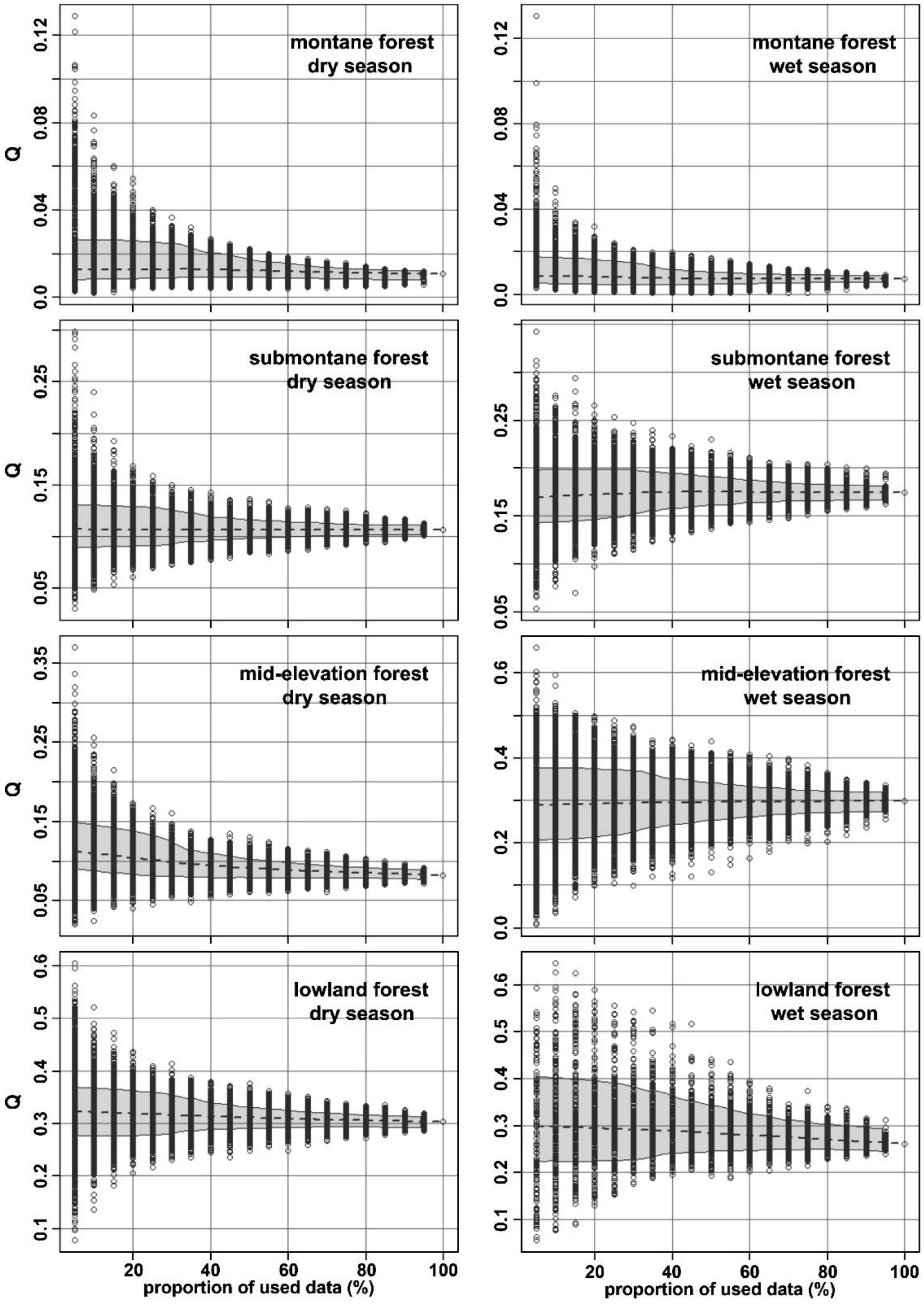

Figure S9. Effects of sampling effort on network modularity (Q). The x-axis shows the proportion of the entire dataset that was used for index calculation. The lines surrounding the grey area are the fits based on the variance function. Note that there was independent smoothing of the squares for the positive and negative residuals from the mean fit, and then the square root of the fitted values was added to the mean fit.

Running title: Altitude-driven floral visitor shifts on *H. revolutum.*

Coping with altitude: Altitude-driven visitor shifts on *Hypericum revolutum* (Hypericaceae) on Mount Cameroon grasslands.

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ABSTRACT

Thanks to the steep changes in various abiotic factors, elevational gradients offer an excellent system to study plasticity in plant-pollinator interactions. Such knowledge is essential for discussing recent ecological and evolutionary hypotheses on plant pollination systems. We can assess how individual plants are specialized, if one pollinator can be replaced by another, and how pollinator-mediated selection pressures act on floral traits. Our study focused on Mount Cameroon, an underexplored biodiversity hotspot, using *Hypericum revolutum* (Hypericaceae) as the model plant. We observed flower visitors across four elevations during two seasons. Birds, bees, and flies have been observed as important groups of floral visitors. Among birds, *Cinnyris reichenowi* (Nectariniidae) has been by far the most frequent visitor. Our findings revealed the same pattern in visitation frequencies, without regard if we considered all bird visitors or just *C. reichenowi*. This pattern was hump-shaped, peaking at approximately 2,700 meters above sea level, and visitation increased during the transition from wet to dry seasons. Male *C. reichenowi* visited flowers more frequently than females. Considering insect visitors, bee and fly activities decreased and did not change respectively with increasing elevation. These results highlight the importance of altitude-driven shifts in pollinator communities, with bees dominating lower elevations, birds dominating mid-elevations, and flies dominating higher elevations. The observed patterns imply potential evolutionary pressures on plants to adapt to the prevalent pollinator species, which could drive local adaptations and diversification within plant populations as predicted by the mosaic of coevolution theory.

Keywords: Afrotropics, elevational gradients, floral visitor shifts, montane grasslands, *Nectariniidae*, nectarivory, pollination.

1. Introduction

Elevational gradients, with their steep abiotic changes over short geographic distances, play a crucial role in structuring biological communities by altering both climatic conditions and resource availability (Körner, 2007; Sponsler et al., 2022). In this sense, elevational biodiversity patterns are relatively well-documented for many animal (e.g., Colwell et al., 2016; Peters et al., 2016; Beck et al., 2017; Maicher et al., 2020) and plant taxa (e.g., Grytnes, 2003; Bruun et al., 2006; Colwell et al., 2016). Additionally, these gradients not only affect biodiversity distribution patterns, but also strongly shape inter-specific interactions, such as plant-pollinator interactions (Maguiña-Conde et al., 2023).

Visitors of a single plant species can differ among individual populations or phenological periods (Thompson, 2005). Plants with broad elevational ranges must adapt locally to pollinator community changes due to the filtering effects of elevation on different pollinator functional groups (Malo & Baonza, 2002). This scenario serves as a template for the geographical mosaic of coevolution between plants and their floral visitors (Anderson & Johnson, 2007). Pollinator turnover is often mediated by temperature as was shown for bees and flies (i.e, bee-to-fly transition; McCabe & Cobb, 2021). In this context, bumblebees, known for being cold-adapted, were identified as the primary pollinators of alpine populations of *Campanula rotundifolia* in the Rocky Mountains (Bingham & Orthner, 1998). Contrastingly, larger bumblebees were found to be replaced by smaller species at higher elevations on *Campanula punctata* (Nagano et al., 2014) and *Prunella vulgaris* (Kuriya et al., 2015) in central Japan. Moreover, higher elevations have shown increased relative frequencies of fly visitors and decreased numbers of bees and beetles in pollination networks (Lay et al., 2013). This pattern has also been confirmed by Sommaggio et al. (2022) which reported an elevation-induced turnover between solitary bees and hoverflies. Therefore, there is a zonation of different pollinator functional groups across elevational gradients due to the physiological constraints of pollinators in coping with harsh mountain top conditions (Adedoja et al., 2018; Lefebvre et al., 2018).

In contrast to insects, birds, as endothermic animals, are much less dependent on ambient temperature, are able to fly in more windy and rainy conditions, and consequently, are less affected by unfavourable weather conditions on mountain tops (Dellinger et al., 2021). For instance, under rainy conditions at high elevations in Mexico, bird-pollinated plants were more effectively pollinated than closely related bee-pollinated species, indicating an altitude driven bee-to-bird transition (Cruden, 1972, but see Delinger et al., 2023). Similarly, Janeček et al. (2022) reported more plants with bird-pollination syndrome to flower during the rainy season on Mt. Cameroon, and Uceda-Gómez et al. (2024) demonstrated that trait matching during this period is more important. Lehmann et al. (2019) observed a shift from butterflies to hummingbirds as the most effective pollinator group of *Gonzalagunia hirsuta* towards higher elevations on Dominica island in the Caribbean. Moreover, pollinator exclusion experiments in the eastern Himalayas demonstrated that several *Rhododendron* species are heavily dependent on sunbirds (Nectariniidae) at high elevations (Huang et al., 2017). Contrastingly, sunbirds showed decreased visitation frequency at higher elevations on the same plant taxa in the Sikkim Himalaya mountains (Basnett et al., 2019).

Our study aimed to explore the relationship between floral visitors (bees, birds, and flies) and elevation in the montane grasslands of Mount Cameroon. We used a dataset on flower visitors of *Hypericum revolutum* (Hypericaceae) across an elevational gradient. Our main aim was to answer the following question: How does the relative visitation of bees, birds, and flies on *H. revolutum* change along the elevational gradient? *H. revolutum* is one of the main nectar sources on the montane grasslands (Bartoš et al., 2012; Janeček et al., 2024). We hypothesise that there will be a turnover of pollinator functional groups across the elevational gradient. Thus, we expect bees to be more frequent floral visitors at the lower elevations, with increasing bird activity at high elevations. Moreover, we hypothesized a shift in insect visitor functional groups across the elevational gradient. In this sense, we expect a turnover from bee to fly dominated visitation. As a secondary aim, given that *Cinnyris reichenowi* (Nectariniidae) is the main bird visitor of *H. revolutum* and is sexually dimorphic, we aimed to explore sexual differences in floral visitation in relation to elevation. Nectar levels in the flowers inside the territory are kept low by frequent bird visits, as observed in other nectar-feeding birds (Feinsinger & Colwell, 1978; Lara et al., 2009). Thus, we expect males of *C. reichenowi* to visit *H. revolutum* plants at a higher rate than females due to competitive exclusion from this nectar rich sources and/or territorial behaviour.

2. Material and Methods

2.1. Study site

The study was conducted on Mount Cameroon (Fig. 1a). The data were collected at four sites along an altitudinal gradient, representing four types of montane grasslands (Fig. 1b): a) low elevation montane grassland around the locality of P&T dominated by tall grass *Loudetia simplex* (c. 2300 m a.s.l.; P&T-1), b) mid-elevation montane grassland also around the locality of P&T representing the transition from tall to short grassland vegetation (c. 2800 m a.s.l.; P&T-2), c) mid-elevation montane grassland around the 1989 lava flow (3200 m a.s.l.), species rich grasslands with typical occurrence of grasses such as *Andropogon* spp., *Sporobolus montanus*, and *Koeleria capensis* , and d) high elevation montane grassland around the locality of Camp 2 (3500 m a.s.l.) with sparse vegetation dominated by *Festuca abyssinica*. Mount Cameroon presents distinct seasonality (Maicher et al., 2020), with a period of water shortage (mid-November to February) combined with a wet season of heavy rains (June to September). Data were collected during two expeditions in two periods: one in the interseason period from wet to dry (November 2021) and once in the interseason from dry to wet season (May 2022); during each expedition all sites were sampled.

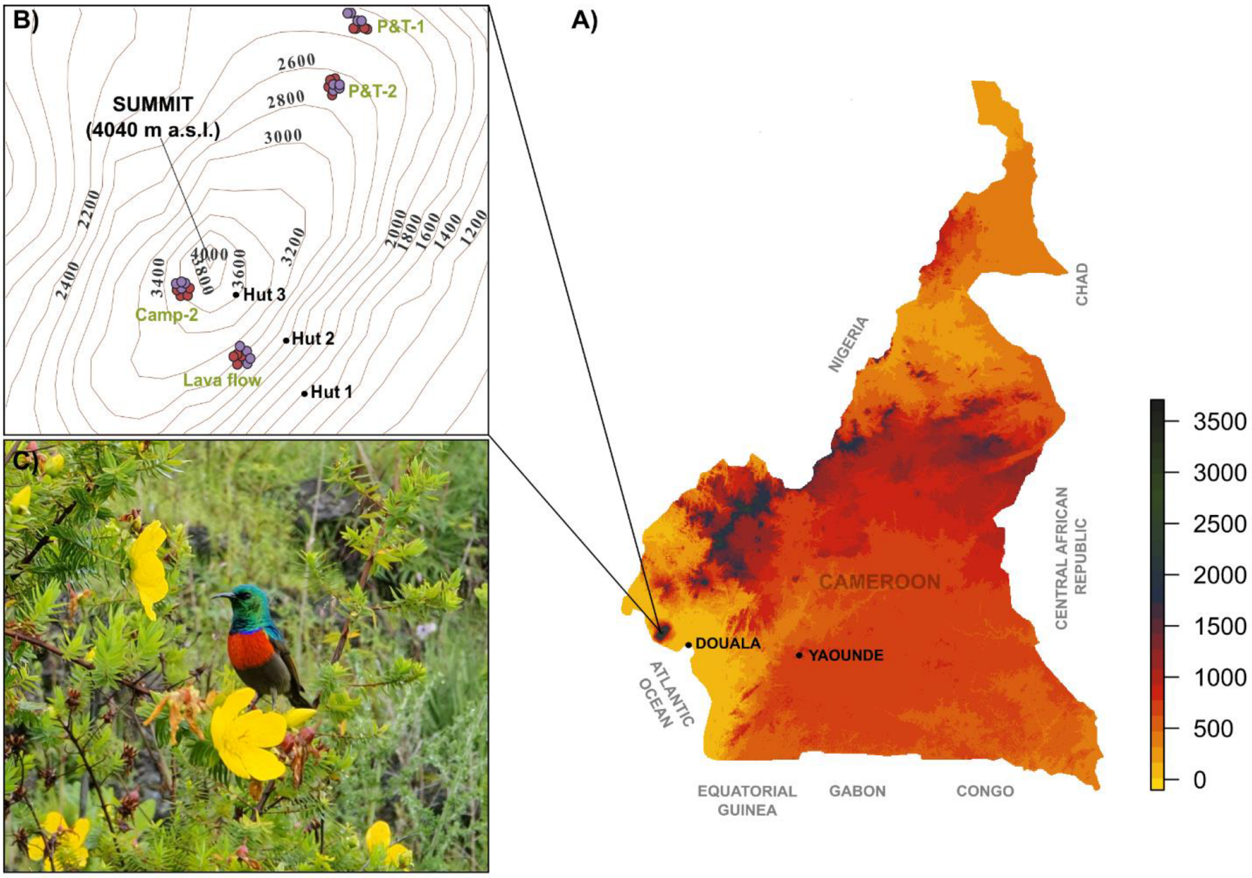

Figure 1. Location of Mount Cameroon and our sampling points within Cameroon: A) Topographical map of Cameroon; B) Topographical map of Mount Cameroon with the geographical position of our sampling locations. Four different elevations were sampled: P&T-1 (c. 2300 m a.s.l.), P&T-2 (c. 2800 m a.s.l.), Lava flow (3200 m a.s.l.), and Camp 2 (3500 m a.s.l.) The different colours represent the two periods sampled: transition season from wet to dry (in red) and from dry to wet (in purple); C) Male *Cinnyris reichenowi* (Northern double-collared sunbird) visiting the flowers of *Hypericum revolutum* (Photo credit: Štěpán Janeček).

2.2. Study species

Our target plant species was *Hypericum revolutum* (Hypericaceae; Fig. 1c). *H. revolutum* is a shrub or small tree of open forest, forest margins and montane woodland and grasslands, native to the Arabian Peninsula and Africa (Robson, 1961). On Mount Cameroon it is commonly found at altitudes between 2000 and 3700 m a.s.l (personal observation). Single bright yellow flowers form at the ends of branches, up to 5 cm in diameter.

The main bird visitor of *Hypericum revolutum* on Mount Cameroon montane grasslands is *Cinnyris reichenowi* (Fig. 1c). On Mount Cameroon, individuals of this sunbird weigh 7–10 g and have a bill length of 1.6–2.2 cm (Sejfová et al., 2021). *Cinnyris reichenowi* has a very wide elevational range, occurring from 1100 (Janeček et al., 2024) up to 2780 m a.s.l on Mount Cameroon (Cheke et al., 2001).

2.3. Observation of plant-bird and plant-insect interactions

Plant-bird interactions were recorded by direct observation of bird visitors. Due to the openness of the landscape, we observed at least 10 shrubs at the same time. We observed each shrub during an eight hour period. At each elevation, we aimed to observe 40 shrubs of our target plant species. We carried out observations during two consecutive days at each elevation. We chose those shrubs whose flowers were fresh and recently opened. Observations were made simultaneously by two observers which were seated at least 100 m apart to avoid recording the same bird visitor twice. We recorded all bird visitors to the species level. Moreover, when possible, we recorded the sex of the visitors. Due to difficulties to find flowering plants at some elevations the number of observed plants differ between each elevation.

We calculated bird visitation frequencies per shrub individual as follows:

$$Visitation\ frequency = \left(\frac{n^{\underline{o}}\ of\ visits}{observed\ time}\right)$$

thus, we obtained a visitation frequency that is standardized by the number of hours so all the plant shrubs can be compared.

To estimate the abundance of insect visitors across the elevational gradient, we counted the total number of insects present in the flowers of each shrub. The counting took place three times per day (i.e., morning, noon, afternoon) and in all the plants observed. Moreover, insect visitors were classified to functional groups: bees or flies. From every plant observed we also recorded the number of flowers, thus, insect visitation was estimated as the abundance of insects per flower, as follows:

$$Insect\ abundance = \left(\frac{n^{\underline{o}}\ of\ insects}{n^{\underline{o}}\ of\ flowers}\right)$$

2.4. Statistical analysis

To explore the general patterns along the elevational gradient in bird visitation we firstly fit our dataset to *Generalized Additive Models (GAM,* Wood 2006*)* opting for a hurdle approach. GAM models avoid the explicit specification of a functional form for the relationship between the response variable and predictor variable, allowing the identification of nonlinear relationships without the need for subjective and pre-determined model specifications. Instead, nonparametric smoothers (i.e., splines) are employed to depict the relationship, offering flexibility and adaptability in capturing complex patterns (Wood 2006). Hurdle models are suitable for zero inflated datasets.

First, we dummy coded with zeros and ones bird visitation to calculate the probability of visitation in relation to elevation ($\boldsymbol{GAM_{I}}$). We set the distribution to binomial with a logit link. For the non-zero continuous part (visitation; $\mathbf{GAM}_{\mathbf{II}}$), we set the distribution to "gamma" with a link function and modelled the frequency of bird visitation. In both models, fixed factors were elevation (with a smoothing term), number of flowers, and study period (i.e., wet-dry or dry-wet). Second, and since, most of the visits recorded were made by *Cinnyris reichenowi* a third *GAM* model (**GAM_{III}**), with the same settings as model $GAMM_I$, to model the probability of visitation across the elevational gradient by *C. reichenowi* individuals. Third, since *C. reichenowi* is a highly dimorphic species we aimed to investigate the effects of sex on bird visitation. Hence, a fourth GAM (**GAM_{IV}**) model was built to account for differences in the frequency of visitation of each sex. This model included elevation (with a smoothing term), number of flowers, study period, and sex as fixed effects. In $\mathrm{GAMM}_{\mathrm{II}}$ and $GAMM_{\mathrm{IV}}$ the response variable was frequency of visitation. Last, to explore the interactive effects of season and sex a fifth GAM model (**$GAM_{V\text{-}VI}$**) was built. The structure of this model was the same as model **$\mathrm{GAM}_{\mathrm{I}}$** and **$\mathrm{GAM}_{\mathrm{III}}$**. In this model, the response variable was the probability of visitation by each sex.

We also created another set of GAMM models to explore the effects of elevation and study period on the abundance of insects. First, we ran a logistic regression to predict the effects of elevation on the presence of insects across the elevational gradient (**GAM_A**). We set the distribution to binomial with logit link. Further, we ran another GAM model (**GAM_B**) with only the plants in which insects were found. In this model, the response variable was insect abundance per flower in each observed plant. The distribution was set to Poisson with a log link. In both models, fixed factors were elevation (with a smoothing term), number of flowers, and study period. Further, to explore insect functional group shifts across the elevation we fit another GAM model (**GAM_C**). We set the distribution to binomial with logit link. In this model, the proportion of flies relative to bees was used as a response variable. Fixed factors were elevation (with smoothing term), number of flowers and study period. Finally, to explore the activity of the different insect functional groups across the elevational gradient, we ran separate models for bees and flies (**$\mathrm{GAM}_{\mathrm{D\text{-}G}}$**) with the same specifications as model A and B.

In all models (i.e., $GAMM_{I\text{-}IVI}$ and $GAMM_{A\text{-}G}$), we reduced the number of splines used to calculate the smoothing term to five (Peters et al., 2019). We used the "*gam*" function from the *mgcv* R package (Wood, 2011) to conduct these analyses. We carried out all the analyses with R software V. 4.2.0 (2022).

3. Results

In total, we recorded 2727 bird visits on *H. revolutum* across the elevational gradient. The visits were performed by five bird species: *Euplectes capensis* (Ploceidae), *Cinnyris bouvieri* (Nectariniidae), *Cinnyris reichenowi* (Nectariniidae), *Linurgus olivaceous* (Fringillidae), and *Zosterops melanocephalus* (Zosteropidae). Two of these species are specialised nectarivores (*C. reichenowi* and *C. bouvieri*), whereas the other three species are generalist passerine birds, mainly feeding on insects found on the flowers or flower parts (personal observation). Of these five species most of the visits were made by *C. reichenowi* (2541 visits, 93.18 % of all visits). *C. reichenowi* was recorded in all elevations during the wet to dry transition period. Nonetheless, it was absent from the highest elevation during the dry to wet transition period. We recorded the highest number of visitors at the locality of P&T-2 (1738 visits; c. 2800 m. a.s.l.). Plants at the lowest and highest localities received very few visitors (50 and 55 visits respectively). Moreover, most the visits recorded happened during the transition period from wet to dry season (e.g., 2311 visits; 84.75% of all the visits recorded). Insect abundance was highest at the two lowest elevations during the dry to wet transition season. Bees were most active at low elevations, whereas the activity of flies remained constant across the elevational gradient. We recorded the highest proportion of bees in the lowest elevation, with more than 75 % of insect visitors being bees. The relative proportion of bees to flies decreased with elevation, with no bees recorded in the highest elevation.

3.1. Bird visitation and its relationship with elevation

The analysis of bird visitation probability in relation to elevation yielded a distinctive hump-shaped pattern. As elevation increased, the probability of bird visitation initially exhibited an upward trend, peaking at an optimal elevation range before gradually declining (Fig. 2a). Moreover, the probability of visitation also increased with the number of flowers each plant had (Fig. 2b). Additionally, we found an effect of the sampling period on the probability of visitation. Plants during the interseason period from wet to dry season, had a higher probability of visitation across the elevational range (Fig. 2a). The non-zero part of the model showed similar results (see Table 1). We also observed a clear peak in visitation frequency at around 2800 m a.s.l. and then a slight decrease towards the higher elevations (Fig.2c). The interseason period from wet to dry had higher visitation frequencies (Fig. 2c).

3.2. Sex-specific visitation pattern on Hypericum revolutum

The probability of visitation by *C. reichenowi* individuals also showed a clear hump-shape pattern in relation to elevation (Supplementary Fig. S1). Moreover, the study period had a significant effect on this probability (Table 1). The probability of visitation by *Cynniris reichenowi* males was not influenced by elevation (Table S1). Sampling period was the only term of the model that influenced the probability of visitation by male individuals (Table S1). Males showed higher probabilities in both interseason periods analysed (Supplementary Fig. S2). Females showed a decrease in the probability of visitation from wet-dry to dry-wet interseason periods. However, this pattern was opposite for males (Supplementary Fig. S2). Elevation together with the number of flowers had a significant effect on the visitation frequency of the species (Table 1). Its visitation frequency also peaked at around 2800 m a.s.l (Supplementary Fig. S3). The term “sex had a nearly significant effect on the frequency of visitation (Table 1).

Table 1. Summary of all GAM models for the bird dataset. Model I include all plants studied, both visited and non-visited. Model II includes only the visited plants, and the frequency of visitation is pooled for all visitors a plant received. Models III and IV only include visits made by *C. reichenowi*. Model III modelled the probability of visitation of *C. reichenowi* individuals, whereas Model IV shows the changes in visitation frequency across the elevation for both sexes of *C. reichenowi.* Significant values are presented in bold.

			Parametric coefficients				**Approximate significance of smoothed terms**				
	Model description	Term	Estimate	Std. Error	t-value	P-value	Term	edf	Ref. df	F-value	P-value
All bird visitors	**I. Probability of visitation - elevation**										
	Family: Binomial	Intercept	-1.771	0.321	-5.505	**0.000**	Elevation	2.784	3.115	59.21	**0.000**
	Link function: logit	Flowers	0.068	0.017	3.912	**0.000**					
		Period	1.055	0.381	2.765	**0.005**					
	II. Frequency of visitation - elevation										
	Family: Gamma	Intercept	-0.835	0.203	-4.104	**0.000**	Elevation	3.057	3.309	17.3	**0.000**
	Link function: log	Flowers	0.065	0.007	8.642	**0.000**					
		Period	0.686	0.222	3.080	**0.002**					
Cinnyris reichenowi	**III. Probability of visitation-elevation**										
	Family: binomial	Intercept	-1.132	0.298	-3.799	**0.000**	Elevation	2.997	3.326	72.07	**0.000**
	Link function: logit	Flowers	0.018	0.012	1.501	0.164					
		Period	0.859	0.353	2.428	**0.015**					
	IV. Frequency of visitation-elevation										
	Family: Gamma	Intercept	-0.792	0.305	-2.594	**0.010**	Elevation	2.918	3.163	12.29	**0.000**
	Link function: log	Flowers	0.056	0.008	6.951	**0.000**					
		Period	0.143	0.274	0.522	0.602					
		Sex	0.384	0.198	1.940	**0.054**					

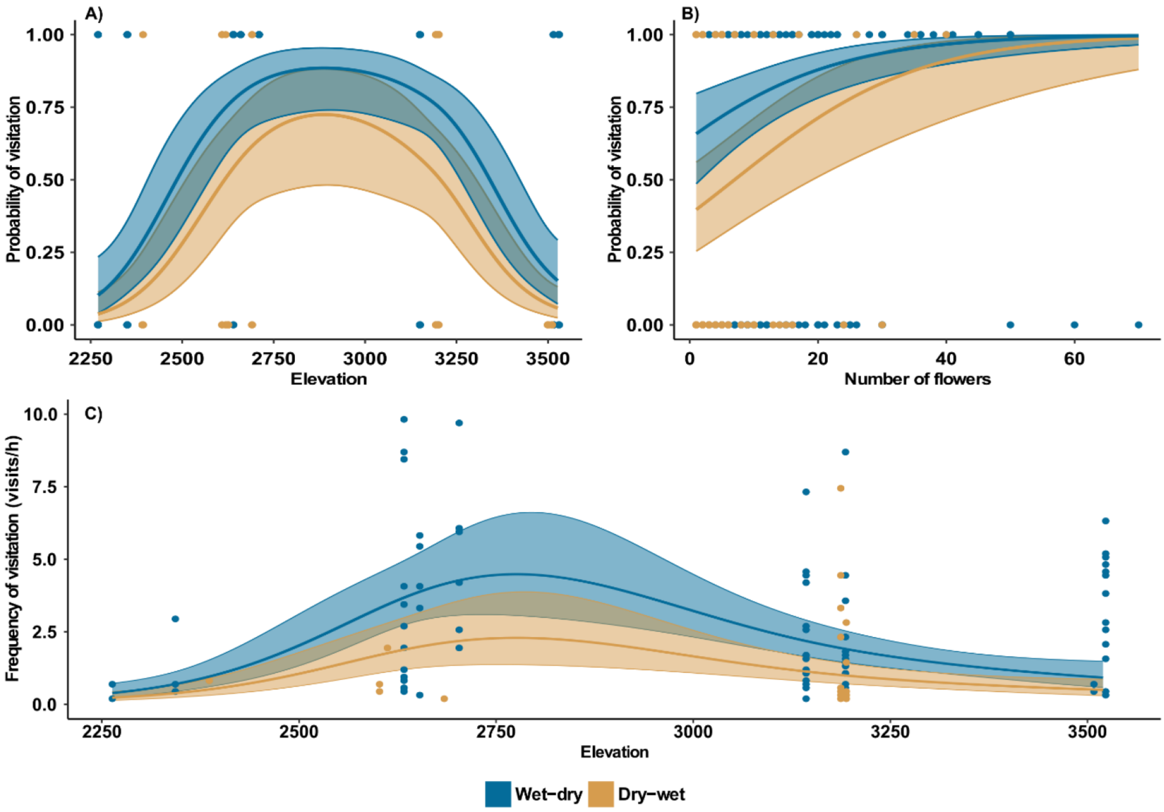

Figure 2. Results from the modelling of the probability of visitation and the frequency of visitation by birds. a) Probability of visitation across the elevational gradient; b) Marginal effect of the number of flowers in the probability of visitation; c) Modelled visitation frequency for visited plants across the elevational gradient. Dots represent the observed interaction frequencies at each sampled elevation. Results are presented for both seasons sampled: interseason from dry to wet season (in light brown), and interseason from wet to dry season (in dark blue).

3.3. Altitude-driven bee-to-fly transition

The logistic regression model, in which we tried to explain the probability of the presence of insects on individual plants, showed that only the number of flowers was a significant factor (Table 2). The probability of finding insect visitors increased with the number of flowers per plant (Supplementary Fig. S4a). When considering only those plants where insects were found, the number of visitors per flower increased with the total number of flowers (Table 2). The highest number of insect visitors was found around 2800 m a.s.l. (Supplementary Fig S4b). The proportion of flies to bees increased with elevation (Table 2; Supplementary Fig. S5). At low elevations more than 75 % of insect visitors were bees. The turnover in insect pollinator functional groups was observed at around 2600 m a.s.l. At high elevations only flies were found, whereas at low elevation bees where more prominent. Moreover, the proportion of flies to bees was higher irrespective of the interseason period considered (Supplementary Fig. S6). When considering each insect functional group separately two main patterns were found. First, the probability of finding bee visitors decreased with elevation (Table 3 and Supplementary Fig. S6). Nonetheless, bee visitation frequencies on visited plants were not influenced by any of the terms included in the model (Table 3). Second, the probability of fly visitation and its frequency were not influenced by elevation (Table 3). Fly activity remained constant across the elevational gradient (Fig. 3). Fly visitation probability increased with the number of flowers and during the dry to wet interseason period, and their abundance per flower increased during the transition season from dry to wet season (Supplementary Fig. S7).

Table 2. Summary of all GAM models run for the insect dataset. Model A includes all plants studied. Model B includes only plant where insects were found. In models A and B, both insect functional groups are analysed together. Model C represents the proportion of flies relative to bees across the elevational gradient. Significant values are presented in bold.

		Parametric coefficients				**Approximate significance of smoothed terms**				
Model description	Term	Estimate	Std. Error	t-value	P-value	Term	edf	Ref. df	F-value	P-value
A. Insect presence-elevation										
Family: Binomial	Intercept	-1.141	0.259	-4.400	**0.000**	Elevation	1.269	1.486	0.426	0.474
Link function: logit	Flowers	0.060	0.014	4.288	**0.000**					
	Period	-0.532	0.346	-1.535	0.125					
B. Insect count-elevation										
Family: Poisson	Intercept	0.115	0.297	0.372	0.710	Elevation	1.000	1.000	0.145	0.703
Link function: log	Flowers	0.066	0.028	-2.293	**0.021**					
	Period	-0.628	0.503	-1.248	0.212					
C. Proportion of flies-elevation										
Family: Binomial	Intercept	2.858	0.936	2.545	**0.002**	Elevation	1.030	1.060	13.95	**0.000**
Link function: logit	Flowers	0.017	0.033	0.164	0.600					
	Period	-2.202	1.030	-1.626	**0.032**					

Table 3. Summary of all GAM models run for the different insect functional groups. Two separate sets of models were run for bees and flies. First the probability of visitation in relation to elevation for each insect functional group (Models D and F), and second the abundance (no. of insects/flower) in relation to elevation (Models E and G). Models D and F include all plants observed, whereas models E and G include only those plants where insects were found. Significant values are presented in bold.

			Parametric coefficients				**Approximate significance of smoothed terms**				
	Model description	Term	Estimate	Std. Error	t-value	P-value	Term	edf	Ref. df	F-value	P-value
Bees	**D. Bee presence-elevation**										
	Family: Binomial	Intercept	-3.959	0.718	-5.511	**0.000**	Elevation	2.764	3.312	13.880	**0.003**
	Link function: logit	Flowers	0.036	0.019	1.902	0.057					
		Period	0.896	0.684	1.309	0.190					
	E. Bee count-elevation										
	Family: Poisson	Intercept	-4.724	1.190	-3.969	**0.000**	Elevation	1.000	1.000	2.739	0.098
	Link function: log	Flowers	-0.005	0.047	-0.106	0.916					
		Period	0.652	1.370	0.476	0.634					
Flies	**F. Fly presence-elevation**										
	Family: binomial	Intercept	-1.109	0.258	-4.297	**0.000**	Elevation	1.000	1.000	1.614	0.204
	Link function: logit	Flowers	0.054	0.013	3.914	**0.000**					
		Period	-0.893	0.358	-2.490	**0.018**					
	G. Fly count-elevation										
	Family: Poisson	Intercept	-1.453	0.274	-5.293	**0.000**	Elevation	1.000	1.000	0.017	0.896
	Link function: log	Flowers	-0.014	0.025	-0.580	0.561					
		Period	-1.470	0.515	-2.851	**0.004**					

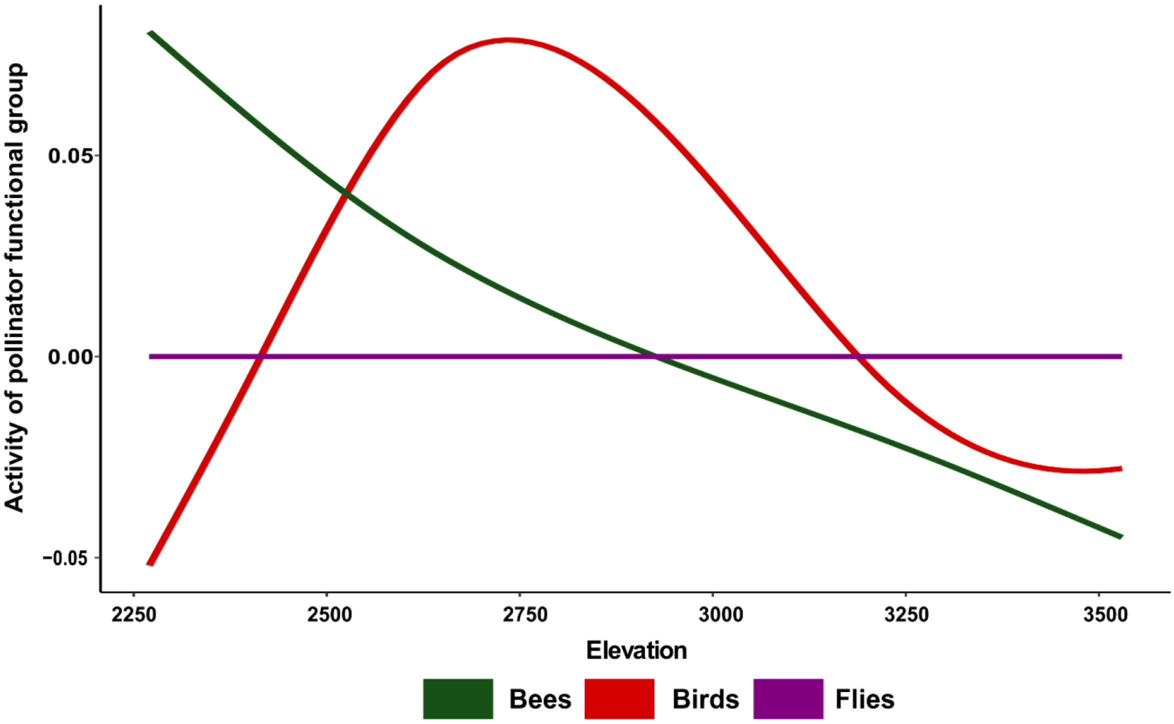

Figure 3. Activity of all the pollinator functional groups across the whole elevational gradient. The fitted curves include both visited and not visited plants at each sampled location. The activity was normalized (mean normalization; (x-mean)/(max-min)) allowing comparison among different kinds of measurements. Pollinator activity is shown in two different ways. Visitation frequency of birds (visits/h; red line), and insect abundance (no. insects/flower) for bees (green line) and flies (purple line). For graphing purposes the fitted lines were produced with a GAM smothing function. For a figure including the observed normalized data points see supplementary material Figure S8.

4. Discussion

Our study confirms the turnover of pollinator functional groups across the elevational gradient. Specifically, bees are the primary visitors to *Hypericum revolutum* at lower elevations, while bird activity increases at higher elevations. The activity of flies remains constant across the gradient. Therefore, the increased proportion of flies at higher elevations is attributed to a decline in bee abundance rather than an increase in fly abundance. Consequently, our findings align with previous studies indicating the dominance of birds and flies in providing pollination services at higher elevations (Cruden 1972; McCabe & Cobb, 2021). These shifts in pollinator functional groups across the elevational gradient present a challenge for *H. revolutum* populations, forcing local adaptation to the varying pollinator community (i.e., mosaic coevolution theory in plant-pollinator interactions; Anderson & Johson, 2007).

Further, we can confirm the difference in visitation frequencies among *C. reichenowi* sexes. We found that male *C. reichenowi* individuals had higher visitation frequencies across the whole elevational gradient. Female probability of visitation dramatically decreased during the dry to wet transition period. These differences are likely due to exploitative competition exerted by males, and downward altitudinal migration by females as pointed out by previous studies (Janeček et al., 2024).

4.1. Bird visitation and its relationship with elevation

Cruden (1972) demonstrated that bee-pollinated plants at high altitudes were less effectively pollinated compared to bird-pollinated plants, suggesting that harsh environmental conditions at high altitudes act as an environmental filter for bee flower visitors. Similarly, our study found a distinct hump-shaped relationship between bird visitation and elevation, with a peak around 2800 m a.s.l. Huang et al. (2017) also observed that sunbirds were more efficient pollinators for *Rhododendron* species at high elevations. Similarly, Hua-Qiang et al. (2021) found that *Eleagnus umbellata* populations living at high elevations were more dependent on sunbirds for providing pollination services. Nonetheless, Basnett et al. (2019) reported the opposite pattern, with bird activity decreasing with increasing elevation. In their study, sunbird abundance decreased at altitudes above the timberline suggesting that those species are restricted to the forest elevational gradient. Contrarily, *C. reichenowi* is a generalised bird species with a wide elevational range expanding from the mid-elevational forest to the high altitude montane grasslands. In fact, our study reports a higher altitudinal maximum for *C. reichenowi* than the previously reported by Cheke et al. (2001). We recorded visits of *C. reichenowi* at 3500 m a.s.l., which is almost 1000 m higher than the previous altitudinal maximum for the species.

Our study did not consider population sizes at each elevation which could also explain the mid-elevation peak. However, two non-mutually exclusive explanations can be given. First, the mid-elevation peak in bird visitation can be the outcome of processes acting at the community level. In our study sites, we observed other generalised bird visitors on *H. revolutum* plants specially at high elevations (personal observation, e.g., *Linurgus olivaceus*, and *Zosterops melanocephalus*)**.** These generalised bird visitors may compete with *C. reichenowi* for nectar resources, making them less abundant at high elevations. Sunbirds are known to be driven by nectar rewards (Chmel et al. 2021), therefore *C. reichenowi* individuals might prefer to forage at mid-elevations where competition is less intense, and nectar resources are higher.

Second, the lower frequencies observed at low elevations may also be attributed to higher resource availability near the montane forest. For example, C. reichenowi individuals might travel between the resource-rich montane forest and the low-elevation montane grasslands. Janeček et al. (2022; 2024) demonstrated that sunbirds feed on ornithophilous plants such as *Impatiens sakeriana* and generalized plants like *Nuxia congesta*, which entail big amounts of nectar in the montane forest.

4.2. Sex-specific visitation pattern on Hypericum revolutum

Besides the middle-elevation peak in bird visitation we also observed sexual differences among *C. reichenowi* individuals. It is well known that nectarivorous birds display territorial behaviour to defend their feeding patches (Cotton, 1998; Justino et al., 2012). In our system, we often observed *C. reichenowi* males engaging in territorial behaviour, excluding not only *C. reichenowi* females but other bird species (i.e., *Zosterops melanocephalus*). These observations could explain female birds' lower visitation frequencies and probabilities, as shown by Lara et al. (2009). On the other hand, females of *C. reichenowi* are less conspicuous, which could affect their detectability.

In addition, the C. *reichenowi* breeding season occurs during the wet-dry transition and dry seasons of Mount Cameroon, and therefore, out of this period, a balance sex-ratio is not necessarily expected. In this sense, altitudinal migrations out of breeding areas are well documented for many bird species (Boyle, 2010; Rappole, 2013; Barçante et al., 2017). Janeček et al. (2024) showed a downward altitudinal migration of *C. reichenowi* females during the wet season of Mount Cameroon. This observation could explain the lower frequencies and probabilities of females observed. Therefore, males will remain in the breeding territories while females would altitudinally migrate, coming back to higher elevations during the reproductive season.

4.3. Altitude-driven bee-to-fly transition

The abundances of Hymenoptera and Diptera along the elevational gradient in our study supported the predicted bee-to-fly transition with increasing elevation, as many previous studies have reported (Peters et al. 2016; Lefebvre et al. 2018; McCabe & Cobb 2021). Our study found that the ratio of flies to bees increased with elevation, with the turnover occurring around 2600 m a.s.l. Diptera species are well known to be better attuned to cooler environments, due to their lower energy requirements and thermoregulatory capabilities (Strathdee & Bale, 1998). On the other hand, hymenopterans are typically associated with warmer and dryer conditions (Devoto et al., 2005).

The observed transition from bee to fly dominance in our study is attributed to a decline in bee activity with increasing elevation, rather than an increase in fly abundance. Classen et al. (2015) found that the number of bee-plant interactions increased linearly with temperature on Mount Kilimanjaro, indirectly supporting our findings. Moreover, Kearns (1992) demonstrated that the predominance of flies on flowers at high elevations appeared to result from a decrease in the presence of other insect orders (e.g., Hymenoptera). Consequently, elevation, serving as a proxy for decreasing temperatures, functions as an environmental filter, excluding bee pollinators from higher altitudes.

This filtering effect of elevation can also help to explain why we observed that the ratio of flies to bees was higher than that of bees irrespective of the study period considered. Our lowest sampling location was at 2250 m a.s.l. Additionally, the ratio of flies to bees had an upward trend during the dry to wet interseason period. This increase in the proportion flies is likely caused by the increased probabilities and abundances observed during this period. Dipteran larvae develop in semi-aquatic and moist conditions (McCabe et al., 2019). Thus, an increase in precipitation during the transition period form dry to wet season can help to explain the observed increase in fly abundances. Nonetheless, this explanation deserves further investigation in the future.

4.4. Evolutionary implications of pollinator functional group turnover across the elevational gradient

The differential distribution of flower visitors along the elevation serves as template for the geographical mosaic of coevolution between *H. revolutum* and its floral visitors (Thompson, 2005). These differences could make floral traits to be subjected to pollinator-driven selection to increase plant reproductive success. For example, Maguiña-Conde et al. (2023) found strong correlation between pollinator and floral traits of *Costus guanaiensis* along a neotropical elevational gradient. Moreover, these authors found how sugar concentration in nectar was more attuned to hummingbird pollination at higher elevations. Additionally, Anderson & Johnson (2007) also found reciprocal coadaptation, which resulted in trait covariation, among the long-tongued fly *Prosoeca ganglbaueri* and its main floral resource. Cuartas-Hernández et al. (2019) also showed how two sympatric *Anthurium* spp. species covaried in their floral traits with their main floral visitors along an elevational gradient in the Colombian Andes.

In our study, despite the prevalence of different pollinator groups across various elevational zones, their actual effectiveness as pollinators remains largely unexplored, and this should be object of next research. Effective pollination and related imposed selection pressures are necessary condition for patterns of trait covariation among pollinators and floral traits. In this sense, two studies demonstrated that bird floral visitors were not necessary pollinators of *H. revolutum* in Bamenda highlands near the timberline where the bees are the main visitors (Janeček et al., 2007; Bartoš et al, 2015), which is in accordance with our observation of bee prevalence in these elevations. Moreover, the contribution of flies to the pollination of *Hypericum revolutum* is also questionable. For example, Bischoff et al. (2013) showed that although flies were the most frequent visitors of plants at high elevations, thy do not collect the pollen needed to provide effective crosspollination. Therefore, in high elevation ecosystems, plants may increasingly rely on self-pollination because of reduced availability of insect pollinators (Totland & Sottocornola, 2001).

4.5. Conclusions

The three functional groups of flower visitors, namely bees, birds, and flies, exhibit distinct distributions along the elevational gradient. Lower elevations appear to be predominantly populated by bees, whereas birds and flies become increasingly significant at mid and high elevations, respectively. This zonation of pollinator functional groups across the elevational gradient is similar to that reported by Adedoja et al. (2018). One question that remains unanswered is how this differing distribution affects plant reproductive success. Therefore, further investigation into the specific roles and effectiveness of each pollinator group is needed. Future research on *H. revolutum* on Mount Cameroon should investigate how pollinator and floral traits may covary across the elevational gradient, potentially driven by coevolutionary processes at the population level. Finally, the role of self- and crosspollination at high elevations should also be investigated.

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5. References

Adedoja, O. A., Kehinde, T., & Samways, M. J. (2018). Insect-flower interaction networks vary among endemic pollinator taxa over an elevation gradient. *PLOS ONE*, *13*(11): e0207453. https://doi.org/10.1371/journal.pone.0207453

Anderson, B., & Johnson, S. D. (2007). The geographical mosaic of coevolution in a plant-pollinator mutualism. *Evol*, *62*(1): 220–225. https://doi.org/10.1111/j.1558-5646.2007.00275.x

Barçante, L., M. Vale, M., & S. Alves, M. A. (2017). Altitudinal migration by birds: A review of the literature and a comprehensive list of species. *J. Field Ornithol.*, *88*(4): 321–335. https://doi.org/10.1111/jofo.12234

Bartoš, M., Janeček, Š., Padyšáková, E., Patáčová, E., Altman, J., Pešata, M., Kantorová, J., & Tropek, R. (2012). Nectar properties of the sunbird-pollinated plant *Impatiens sakeriana*: A comparison with six other co-flowering species. *S Afr J Bot,* 78: 63-74. https://doi.org/10.1016/j.sajb.2011.05.015.

Bartoš, M., Tropek, R., Spitzer, L., Padyšáková, E., Janšta, P., Straka, J., Tkoč, M., & Janeček, S. (2015). Specialization of pollination systems of two co-flowering phenotypically generalised *Hypericum* species (Hypericaceae) in Cameroon. *Arthropod Plant Interact.*, 9: 241-252. https://doi.org/10.1007/s11829-015-9378-8

Basnett, S., Ganesan, R. & Devy, S.M. (2019). Floral traits determine pollinator visitation in *Rhododendron* species across an elevation gradient in the Sikkim Himalaya. Alp Botany 129, 81–94. https://doi.org/10.1007/s00035-019-00225-3

Beck J., McCain , C.M., Axmacher J.C., Ashton, L.A., Bärtschi, F., Brehm, G., Choi, S.W., Cizek, O., Colwell, R.K., Fiedler, K., Francois, C.L., Highland, S., Holloway, J.D., Intachat, J., Kadlec, T., Kitching, R.L., Maunsell, S.C., Merckx, T., Nakamura, A., Odell, E., Sang, W., Toko, P.S., Zamecnik, J., Zou, Y., & Novotny, V. (2017).

Elevational species richness gradients in a hyperdiverse insect taxon: a global metastudy on geometrid moths. *Glob Ecol Biogeogr* 26:412–424. https://doi.org/10.1111/geb.12548

Bischoff, M., Campbell, D. R., Lord, J. M., and Robertson, A. W. (2013). The relative importance of solitary bees and syrphid flies as pollinators of two outcrossing plant species in the New Zealand alpine. *Aust. Ecol.* 38, 169–176. https://doi.org/10.1111/j.1442-9993.2012.02389.x

Bingham, R. A., & Orthner, A. R. (1998). Efficient pollination of alpine plants. *Nature*, *391*(6664): 238–239. https://doi.org/10.1038/34564

Bruun, H.H., Moen, J., Virtanen, R., Grytnes, J.A., Oksanen, L., & Angerbjörn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *J Veg Sci* 17:37–46. https://doi.org/10.1111/j.1654-1103.2006.tb02421.x

Boyle, W. A. (2010). Does food abundance explain altitudinal migration in a tropical frugivorous bird? *Can. J. Zool.*, *88*(2): 204–213. https://doi.org/10.1139/Z09-133

Cheke, R.A., Mann, C.F., & Allen, R. (2001). Sunbirds: A guide to the sunbirds, flowerpeckers, spiderhunters, and sugarbirds of the world. Christopher Helm Publishers.

Chmel, K., Ewome, F. L., Uceda-Gómez, G., Klomberg, Y., Mertens, J. E. J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective. Oikos, 130, 1411–1424. https://doi.org/10.1111/oik.08052

Classen, A., Peters, M. K., Kindeketa, W. J., Appelhans, T., Eardley, C. D., Gikungu, M. W., Hemp, A., Nauss, T., & Steffan-Dewenter, I. (2015). Temperature versus resource constraints: Which factors determine bee diversity on Mount Kilimanjaro, Tanzania? GEB, 24(6): 642–652. https://doi.org/10.1111/geb.12286

Colwell, R.K., Gotelli, N.J., Ashton, L.A., Beck, J., Brehm, G., Fayle, T.M., Fiedler, K., Forister, M.L., Kessler, M., Kitching, R.L., Klimes, P., Kluge, J., Longino, J.T., Maunsell, S.C., McCain, C.M., Moses, J., Noben, S., Sam, K., Sam, L., Shapiro, A.M., Wang , X., & Novotny, V. (2016). Mid-point attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. *Ecol Lett* 19:1009–1022. https://doi.org/10.1111/ele.12640

Cotton, P. A. (1998). Temporal partitioning of a floral resource by territorial hummingbirds. *Ibis*, 140(4): 647–653. https://doi.org/10.1111/j.1474-919X.1998.tb04710.x

Cruden, R. W. (1972). Pollinators in high-elevation ecosystems: Relative effectiveness of birds and bees. *Science*, New Series, 176(4042): 1439–1440.

Cuartas-Hernández, S., Moreno-Betancur, D.J., Gibernau, M., Herrera-Palma, M., & Hoyos-Serna, L. (2019). Contrasting Patterns of Floral Size Variation in Two Sympatric Species of *Anthurium* along an Elevation Gradient in a Tropical Mountain Forest. *I. J. P. S.* 180(3): 209-219. https://doi.org/10.1111/btp.12775

Dellinger, A. S., Hamilton, A. M., Wessinger, C. A., & Smith, S. D. (2023). Opposing patterns of altitude-driven pollinator turnover in the tropical and temperate americas. *Am. Nat.*, 202(2): 152–165. https://doi.org/10.1086/725017

Dellinger, A. S., Pérez-Barrales, R., Michelangeli, F. A., Penneys, D. S., Fernández-Fernández, D. M., & Schönenberger, J. (2021). Low bee visitation rates explain pollinator shifts to vertebrates in tropical mountains. *New Phytol.*, 231(2): 864–877. https://doi.org/10.1111/nph.17390

Devoto, M., Medan, D. & Montaldo, N.H. (2005). Patterns of interaction between plants and pollinators along an environmental gradient. *Oikos*, 109: 461-472. https://doi.org/10.1111/j.0030-1299.2005.13712.x

Feinsinger, P., & Colwell, R. K. (1978). Community organization among neotropical nectar-feeding birds. *Amer. Zool.*, 18(4): 779–795. https://doi.org/10.1093/icb/18.4.779

Grytnes, J.A. (2003). Species-richness patterns of vascular plants along seven altitudinal transects in Norway. *Ecography* (Cop) 26:291–300. https://doi.org/10.1034/j.1600-0587.2003.03358.x

Huang, Z.-H., Song, Y.-P., & Huang, S.-Q. (2017). Evidence for passerine bird pollination in Rhododendron species. *AoB PLANTS*, 9(6): https://doi.org/10.1093/aobpla/plx062

Janeček, Š., Uceda-Gómez, G., Janečková, P., Tropek, R., Tajaocha Fominka, N., Mokake Njie, M., Mílikovský, J., Mekuate Kamga, S., Lyonga Molua, L., & Luma Ewome Francis. (2024) Food resource partitioning between males and females of Volcano Sunbird *Cinnyris preussi* on Mount Cameroon. J. Ornithol. https://doi.org/10.1007/s10336-024-02187-8

Janeček, Š., Chmel, K., Mlíkovský, J., Uceda-Gómez, G., Janečková, P., Fominka, N.T., Mokake Njie, M., Ewome Luma, F. (2022). Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. *Oecologia* 199, 885–896. https://doi.org/10.1007/s00442-022-05234-4

Janeček, Š., Hrázský, Z., Bartoš, M., Brom, J., Reif, J., Hořák, D., Bystřická, D., Riegert, J., Sedláček, O., & Pešata, M. (2007). Importance of big pollinators for the reproduction of two *Hypericum* species in Cameroon, West Africa. Afr. J. Ecol., 45(4): 607–613. https://doi.org/10.1111/j.1365-2028.2007.00779.x

Justino, D. G., Maruyama, P. K., & Oliveira, P. E. (2012). Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. *J. Ornithol.*, 153(1): 189–197. https://doi.org/10.1007/s10336-011-0726-x

Kearns, C. A. (1992). Anthophilous Fly Distribution Across an Elevation Gradient. T*he American Midland Naturalist*, 127(1), 172–182. https://doi.org/10.2307/2426332

Körner, C. (2007). The use of 'altitude' in ecological research. *TREE*, 22(11): 569–574. https://doi.org/10.1016/j.tree.2007.09.006

Kuriya, S., Hattori, M., Nagano, Y., & Itino, T. (2015). Altitudinal flower size variation correlates with local pollinator size in a bumblebeepollinated herb, *Prunella vulgaris* L. (Lamiaceae). *J Evol Biol* 28:1761–1769. https ://doi.org/10.1111/jeb.12693

Lara, C., Lumbreras, K., & González, M. (2009). Niche partitioning among hummingbirds foraging on *Penstemon Roseus* (Plantaginaceae) in central Mexico. *Ornitol. Neotrop.*, 20: 81–91.

Lay, C.R., Linhart, Y.B., & Diggle, P.K. (2013). Variation among four populations of *Erysimum capitatum* in phenotype, pollination and herbivory over an elevational gradient. *Am Midl Nat* 169:259– 273.https://www.jstor.org/stable/23525689

Lefebvre, V., Villemant, C., Fontaine, C., & Daugeron, C. (2018). Altitudinal, temporal and trophic partitioning of flower-visitors in Alpine communities. *Sci. Rep.*, 8(1): 4706. https://doi.org/10.1038/s41598-018-23210-y

Lehmann, L.J., Maruyama, P.K., Joaquim Bergamo, P., Maglianesi M.A., Rahbek, C., Dalsgaard, B. (2019) Relative effectiveness of insects versus hummingbirds as pollinators of Rubiaceae plants across elevation in Dominica, Caribbean. *Plant Biol* 21:738–744. https://doi.org/10.1111/plb.12976

Maguiña-Conde, R., Zuñiga-Rivas, D., & Kay, K. M. (2023). An elevational gradient in floral traits and pollinator assemblages in the Neotropical species *Costus guanaiensis var. Tarmicus* in Peru. *Ecol. Evol*, 13(8): 1–18. https://doi.org/10.1002/ece3.10314

Maicher, V., Sáfián, S., Murkwe, M., Delabye, S., Przybyłowicz, Ł., Potocký, P., Kobe, I. N., Janeček, Š., Mertens, J. E. J., Fokam, E. B., Pyrcz, T., Doležal, J., Altman, J., Hořák, D., Fiedler, K., & Tropek, R. (2020). Seasonal shifts of biodiversity patterns and species' elevation ranges of butterflies and moths along a complete rainforest elevational gradient on Mount Cameroon. *J. Biogeogr.*, 47(2): 342–354. https://doi.org/10.1111/jbi.13740

Malo, J.E., & Baonza, J. (2002). Are there predictable clines in plant-pollinator interactions along altitudinal gradients? The example of *Cytisus scoparius* (L.) Link in the Sierra de Guadarrama (Central Spain). *Divers Distrib* 8:365–371. https://doi.org/10.1046/j.1472-4642.2002.00161.x

McCabe, L. M., Cobb, N. S., & Butterfield, B. J. (2019). Environmental filtering of body size and darker coloration in pollinator communities indicate thermal restrictions on bees, but not flies, at high elevations. *PeerJ* 7:e7867. https://doi.org/10.7717/peerj.7867

McCabe, L. M., & Cobb, N. S. (2021). From Bees to Flies: Global shift in pollinator communities along elevation gradients. *Front. ecol. evol.*, 8: 626124. https://doi.org/10.3389/fevo.2020.626124

Nagano, Y., Abe, K., Kitazawa, T., Hattori, M., Hirao, A.S., & Itino, T. (2014). Changes in pollinator fauna affect altitudinal variation of floral size in a bumblebee-pollinated herb. *Ecol Evol* 4:3395–3407. https://doi.org/10.1002/ece3.1191

Peters, M.K., Peisker, J., Steffan-Dewenter, I, & Hoiss, B. (2016). Morphological traits are linked to the cold performance and distribution of bees along elevational gradients. *J Biogeogr* 43:2040–2049. https://doi.org/10.1111/jbi.12768

Peters, M. K., Hemp, A., Appelhans, T., Becker, J. N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Kühnel, A., Mayr, A. V., Mwangomo, E., … Steffan-Dewenter, I. (2019). Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature*, 568(7750): 88–92. https://doi.org/10.1038/s41586-019-1048-z

Pi, H.-Q., Quan, Q.-M., Wu, B., Lv, X.-W., Shen, L.-M. and Huang, S.-Q. (2021). Altitude-related shift of relative abundance from insect to sunbird pollination in *Elaeagnus umbellata* (Elaeagnaceae). *J. Syst. Evol.*, 59: 1266-1275. https://doi.org/10.1111/jse.12685

R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing

Rappole, J. H. (2013). The Avian Migrant: The Biology of Bird Migration (p. 464 Pages). Columbia University Press.

Robson, N.K.B. (1961). Guttiferae. In: Exell, A.W., Wild, H. (eds). Flora Zambesiaca. Kew Publishing and Flora Zambesiaca Managing Committee, London

Sejfová, Z., Mlíkovský, J., Ewome, F. L., Janečková, P., Klomberg, Y., Njie, M. M., & Janeček, Š. (2021). Sunbirds' tendency to hover: The roles of energetic rewards, inflorescence architecture and rain. *J. Avian Biol.*, 52(7): jav.02818. https://doi.org/10.1111/jav.02818

Strathdee, A. T., & Bale, J. S. (1998). Life on the edge: insect ecology in arctic environments. Annual review of entomology, 43, 85–106. https://doi.org/10.1146/annurev.ento.43.1.85

Sommaggio, D., Zanotelli, L., Vettorazzo, E., Burgio, G., & Fontana, P. (2022). Different distribution patterns of hoverflies (Diptera: Syrphidae) and bees (Hymenoptera:

Anthophila) along altitudinal gradients in Dolomiti Bellunesi National Park (Italy). *Insects*, 13(3): 293. https://doi.org/10.3390/insects13030293

Sponsler, D. B., Requier, F., Kallnik, K., Classen, A., Maihoff, F., Sieger, J., & Steffan-Dewenter, I. (2022). Contrasting patterns of richness, abundance, and turnover in mountain bumble bees and their floral hosts. *Ecology*, 103(7): e3712. https://doi.org/10.1002/ecy.3712

Thompson, J.N. (2005). The geographic mosaic of coevolution. University of Chicago Press, Chicago

Totland, Ø., & Sottocornola, M. (2001). Pollen limitation of reproductive success in two sympatric alpine willows (Salicaceae) with contrasting pollination strategies. *Am. J. Bot.* 88, 1011–1015. https://doi.org/10.2307/2657082

Uceda-Gómez, G., Chmel, K., Janečková, P., Mlíkovský, J., Klomberg, Y., Ewome, F.L., Molua, L.L., Njie, M.M., Tropek, R., Janeček, J. (2023). Drivers of sunbird-plant interactions on Mount Cameroon: between neutrality and niche-based processes. *Biotropica*, 56: 143-148. https://doi.org/10.1111/btp.13290

Wood, S. N. (2006). Generalized Additive Models: An Introduction with R. Chapman & Hall and CRC, Boca Raton.

Wood, S. N. (2011). Generalized additive models: An introduction with R (Second edition). CRC Press/Taylor & Francis Group.

SUPPORTING INFORMATION CHAPTER VII

Uceda-Gomez, G., Molua, L.L., Mani, F.T., Ewome, F.L., & Janeček, Š. (manuscript under review; Journal of Plant Ecology) Coping with altitude: Altitude-driven visitor shifts to *Hypericum revolutum* (Hypericaceae) on Mount Cameroon grasslands.

ELECTRONIC SUPPLEMENTARY MATERIAL

Running tittle: Altitude-driven floral visitor shifts on *H. revolutum*

Coping with altitude: Altitude-driven visitor shifts on *Hypericum revolutum* (Hypericaceae) on Mount Cameroon grasslands.

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Table S1. Summary of the GAM model predicting the probability of visitation by males of *C. reichenowi* (***GAM$_{V\text{-}VI}$***). Male visitation was coded as one, whereas female visitation was coded as zero. The opposite model was also run. Only the one for males is presented.

		Parametric coefficients				**Approximate significance of smoothed terms**				
Model description	Term	estimate	Std. Error	t-value	P-value	Term	edf	Ref. df	F-value	P-value
Probability of visitation male -elevation										
Family: Binomial	Intercept	3.123	1.029	3.033	**0.002**	Elevation	1.776	2.227	0.328	0.785
Link function: logit	Flowers	-0.005	0.015	-0.377	0.706					
	Period	-2.747	1.051	-2.613	**0.008**					

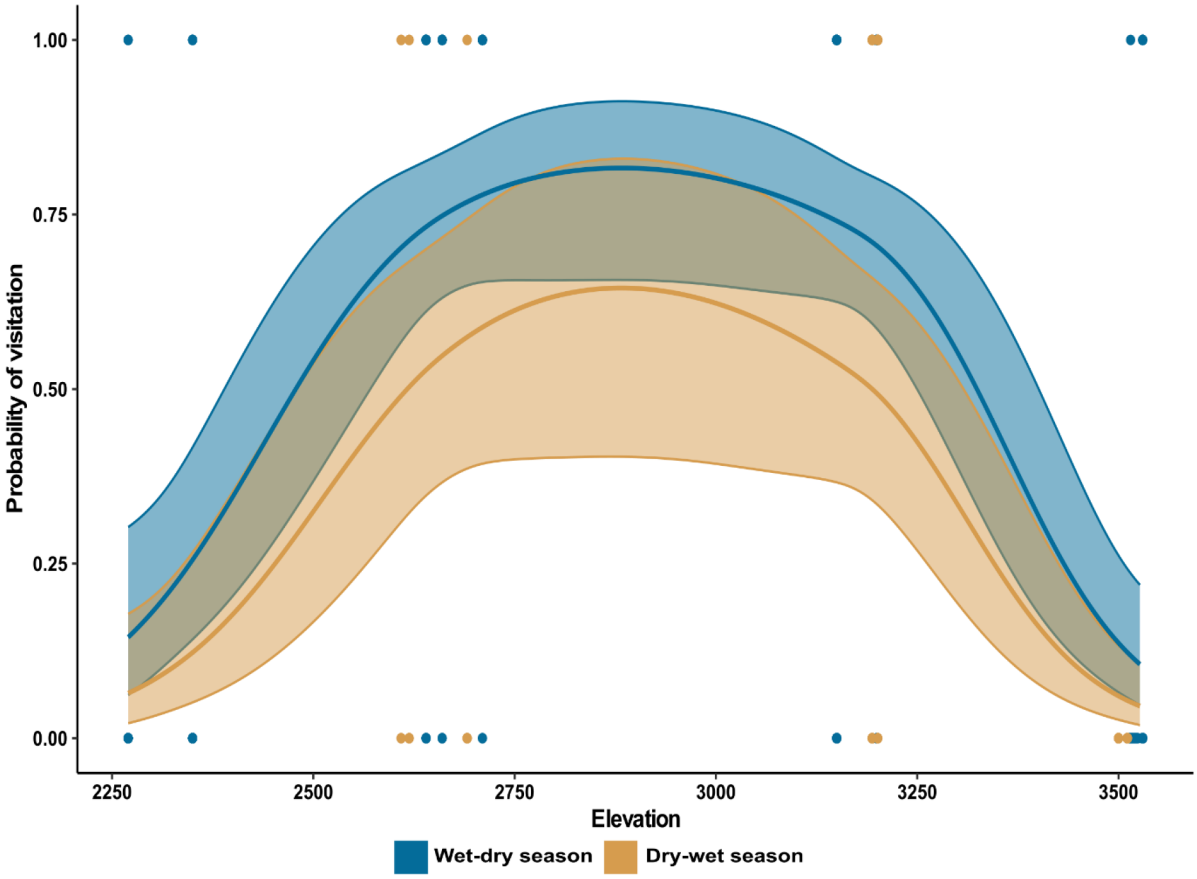

Figure S1. Probability of visitation across the elevation gradient by individuals of *Cinnyris reichenowi*. Dots represent the observed probability values at each sampled elevation. Results are presented for the two periods sampled: interseason from dry to wet season (in light brown), and interseason from wet to dry season (in dark blue). The solid line represents the estimated probability by the GAM_{III} model, whereas the shaded area represents the confidence interval.

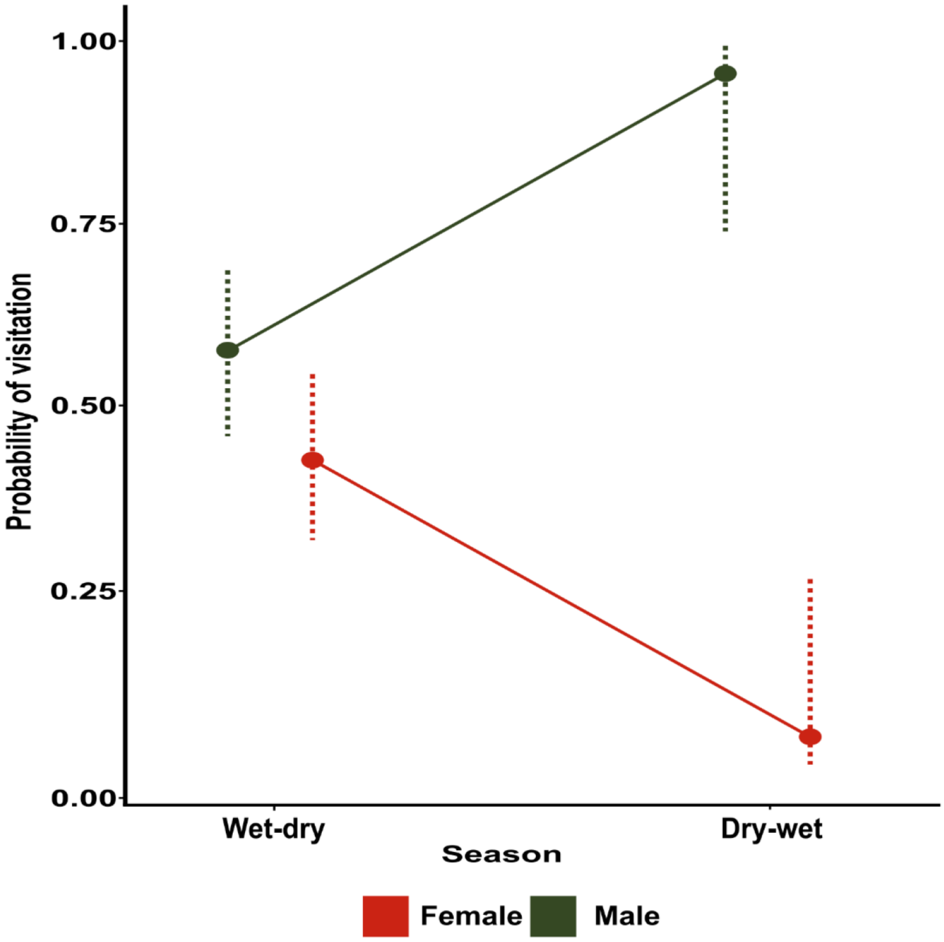

Figure S2. Marginal effects of season on the probability of visitation of each sex of *C. reichenowi*. Dotted lines represent the confidence intervals calculated by the model. Solid dots represent the estimated probability of visitation in each study period. Solid lines represent the trend between the two study periods.

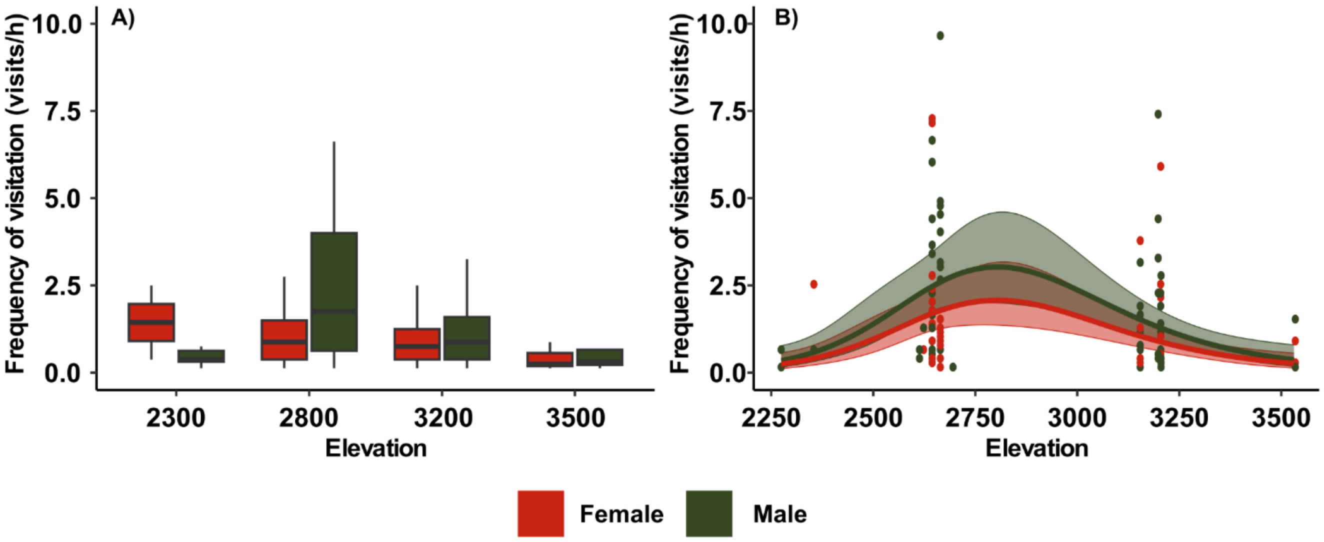

Figure S3. Visitation frequency (visits/h; A), and results of the GAM model (B) for *C. reichenowi* across the elevational gradient. The shade areas represented the confidence interval based on the model parameters and the dots represent the observed values for both males and females.

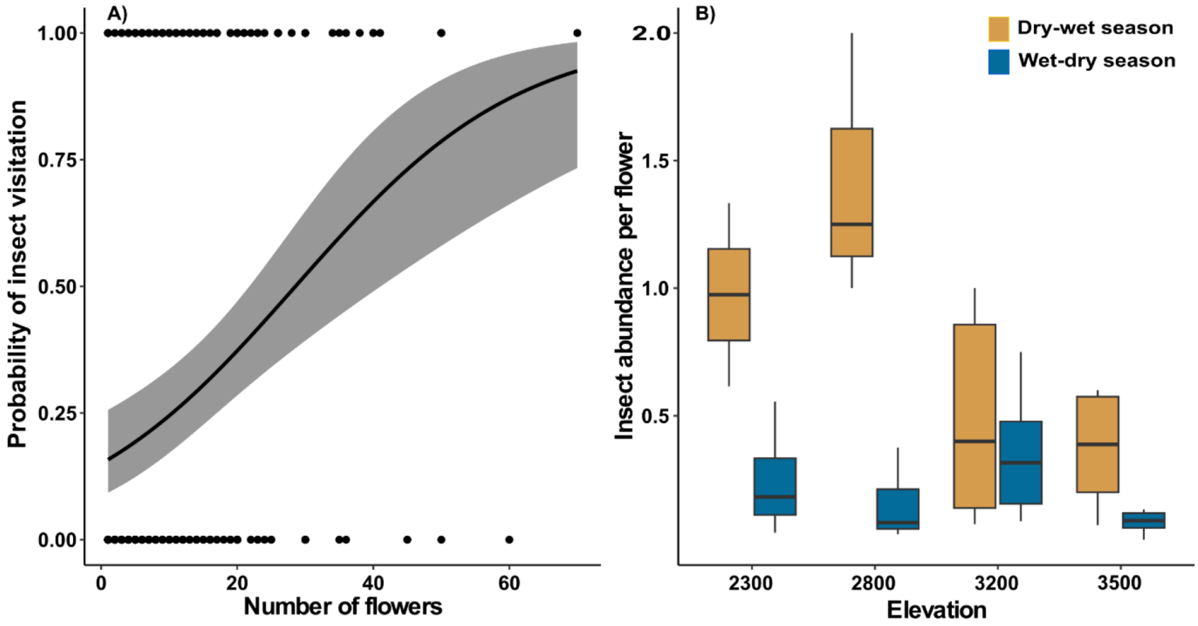

Figure S4. Results from the insect visitor dataset. A) Marginal effect of the number of flowers on the presence/absence of insect visitors. B) Distribution of insect counts at each sampled location for those plants where insects were found.

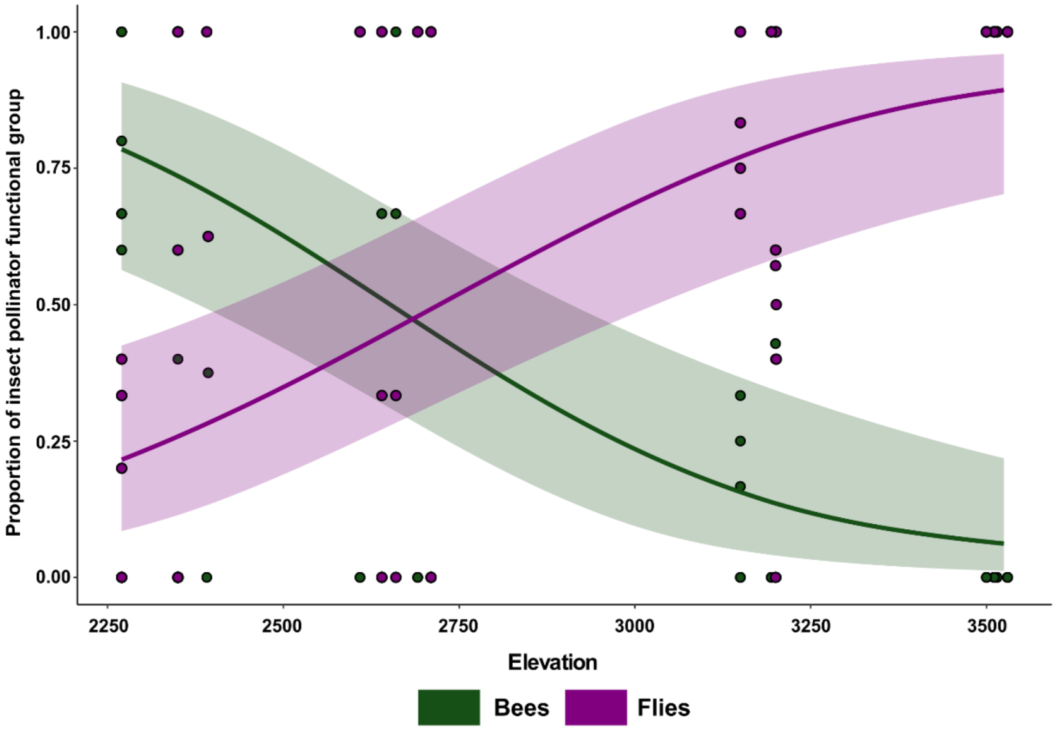

Figure S5. Change in the relative proportion of insect functional groups across the whole elevation gradient. The proportion of bees to flies becomes higher at high elevations, as predicted by the bee-to-fly transition. The fitted curves correspond to the model predictions of Model C (see methods section for a description of this model). Shaded areas correspond to the confidence intervals of the model.

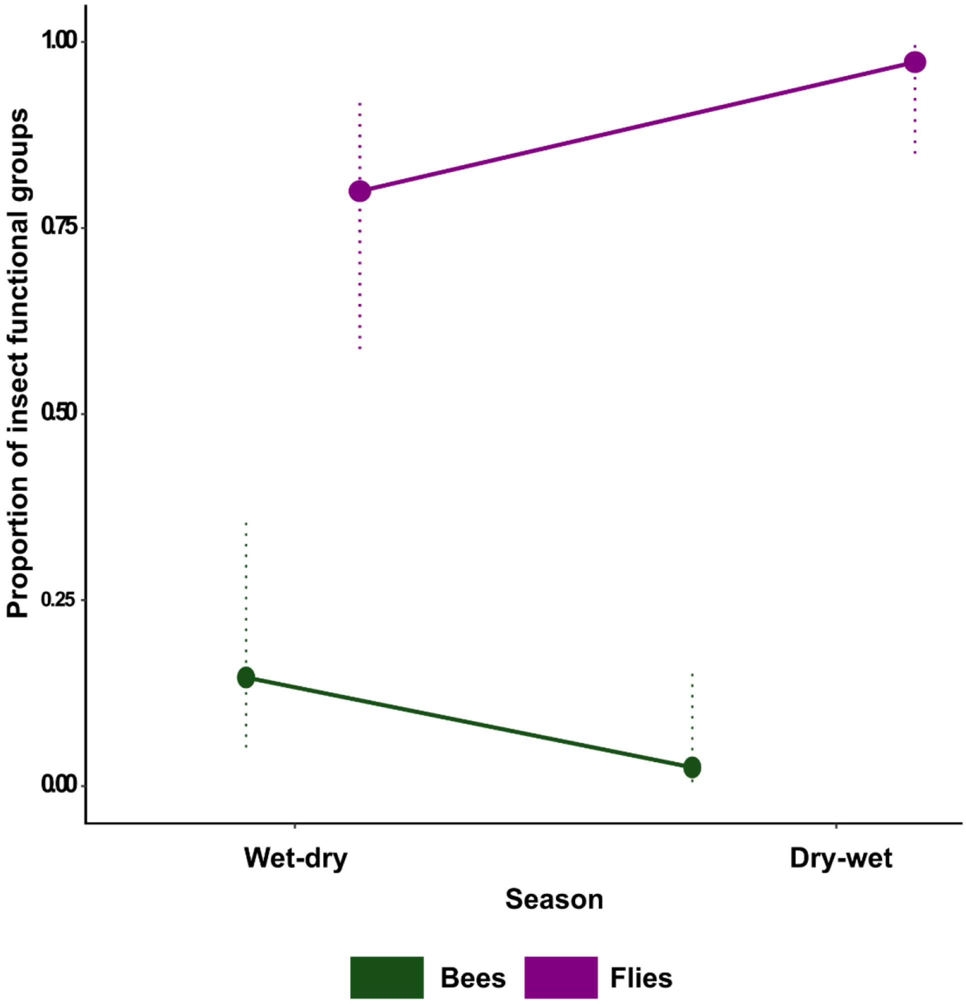

Figure S6. Change in the relative proportion of insect functional groupsamong the interseason periods studied. The fitted curves correspond to the model predictions of Model C (see methods section for a description of this model). Dotted lines correspond to the confidence intervals of the model.

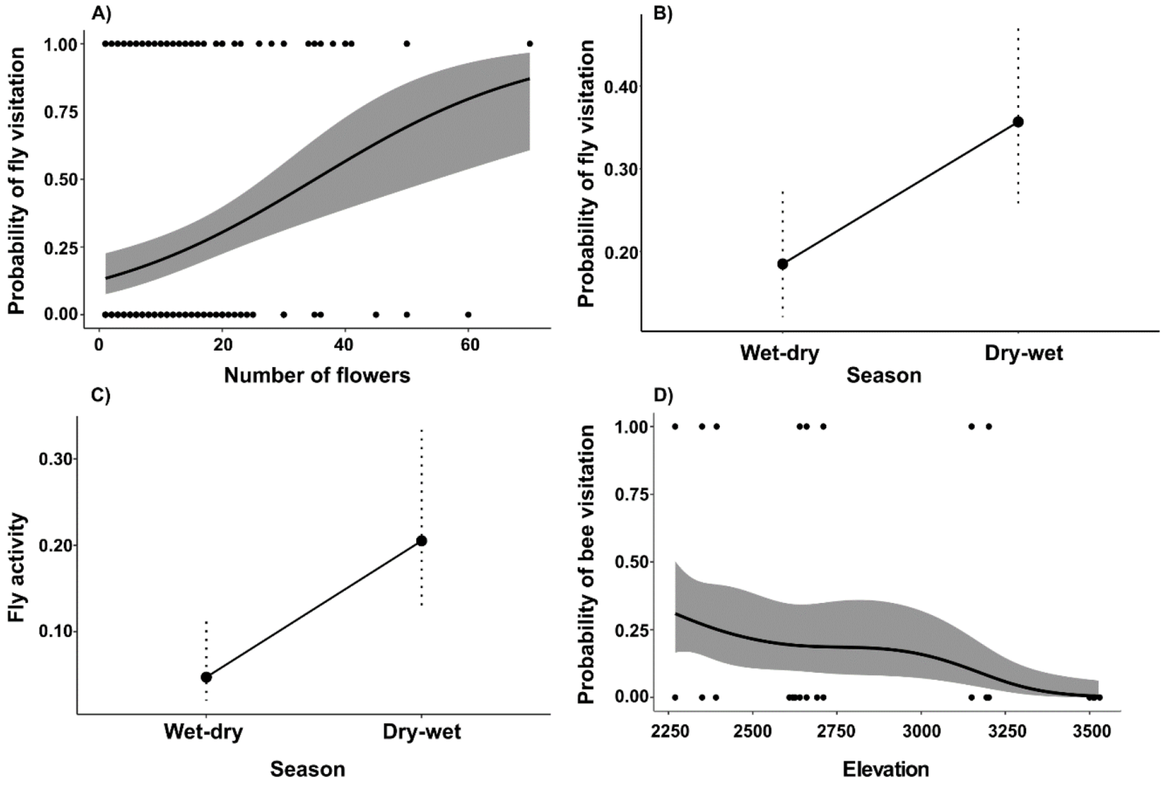

Figure S7. Results from the GAM models fitted for flies (A,B, & C), and flies (D) separately. A) Marginal effect of the number of flowers on the presence/absence of fly visitors. B) Marginal effect of study period on the presence/absence of fly visitors. The solid lines represent the prediction of the GAM model; dotted lines represent the confidence intervals of the model. C) Marginal effect of study period on the activity (no. flies/no. flowers) of ly visitors. D) Marginal effect of elevation on the presence/absence of bee visitors. The shaded are represents the confidence interval of the model.

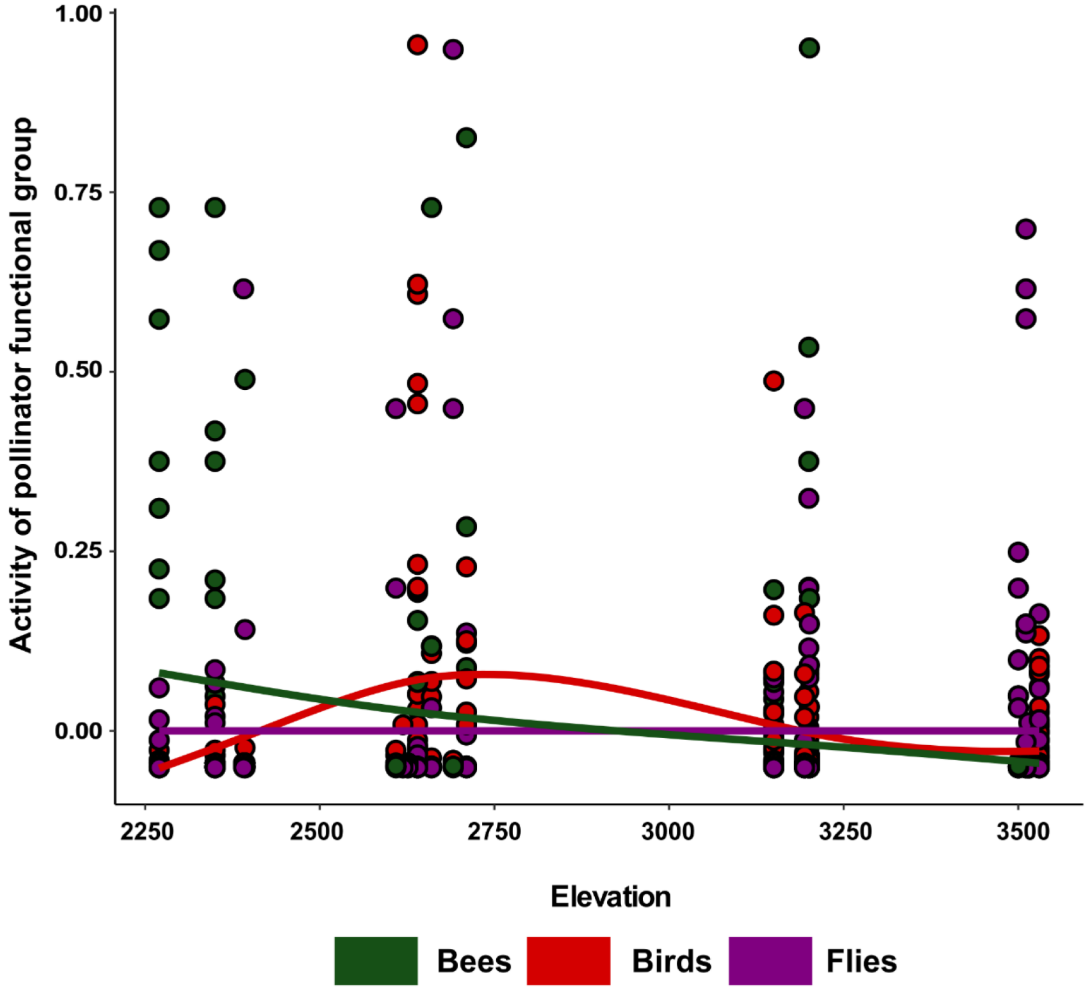

Figure S8. Activity of all the pollinator functional groups across the whole elevational gradient. The fitted curves include both visited and not visited plants at each sampled location. The activity was normalized (mean normalization; (x-mean)/(max-min)), allowing comparison among different kinds of measurements. Pollinator activity is shown in two different ways. Visitation frequency of birds (visits/h; red line), and insect abundance (no. insects/flower) for bees (green line) and flies (purple line). For graphing purposes the fitted lines were produced with a GAM smothing function. The dots represent the observed normalized activities of each pollinator functional group.

Cyanomitra oritis visiting *Impatiens sakeriana*

Guillermo Uceda-Gómez

ECOLOGIST

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PROFILE

I am an early stage researcher with training and experience in the fields of tropical ecology, community ecology and pollination ecology. Currently, I am about to finish my PhD at Charles University, where my research has focused on the drivers of sunbird-plant interactions, and their spatiotemporal variability.

I would like to expand my knowledge to know how pollination affects plant population genetic structure. Moreover, I would like to research on how human-induced disturbance or climate change affect pollination networks in the tropics.

ACADEMIC BACKGROUND

PhD candidate. Ecology | Charles University of Prague, Prague, Czech Republic (To be defended in mid-October 2024)

Project title: Organization of Afrotropical plant-bird pollination communities: the effects of altitude and seasonality. Supervised by **Štěpán Janeček** & **David Hořak**

Topics: pollination biology, altitudinal gradients, seasonality, coevolution, plant-bird interactions, *Nectariniidae*, bipartite networks, trait-matching, pollinator shifts

Skills: Null modelling, probabilistic models, ordination, network analysis, General Additive Models, Next Generation Sequencing, R programming

MSc Environmental Biology. Animal Ecology & Behavioural Ecology (120 ECTS) | Utrecht University, Utrecht, The Netherlands (2015 – 2017)

Major research thesis title: Comparative Energy budgets. The case of the barnacle goose (Branta leucopsis). Supervised by **Thomas Lameris** & **Götz Eichhorn** | NIOO-KNAW, Wageningen, The Netherlands (2015-2016)

Topics: energy budgets, climate change, bird migration, breeding season, moulting period, comparative study, breeding range expansion

Skills: R programming, nest monitoring, digestibility markers, behavioural observations, nitrogen content, diet analysis, artic expedition

Minor research thesis tittle: Reproductive success in the Iberian Lynx (*Lynx pardinus*): Effects of prey abundance, individual age and population sex-ratio. Supervised by **Alfonso San Miguel Ayanz** | Technical University of Madrid, Madrid, Spain (2017)

Topics: species conservation, resource availability, extinction, ecosystem functioning, reproductive biology, LIFE project

Skills: R programming, species monitoring, literature review

BSc Biology. Evolution and Biodiversity (240 ECTS) | Autonomous University of Madrid, Madrid, Spain (2009-2014)

Erasmus Scholarship. Alpine Biodiversity & Conservation (60 ECTS) | Telemark University College, Norway (2012-2013)

Thesis title: Antipredator behavior of domestic and wild ungulates. Supervised **Isabel Barja Nuñez**

Topics: antipredator behavior, wild and domestic ungulates, evolution

Skills: R programming, behavioural observations, scent manipulation

OTHER PROJECTS AND COLLABORATIONS

Reconstruction of bird-plant interaction networks through metabarcoding | Natural History Museum University Denmark, Botany Section, University of Copenhagen (2024)

Principal investigator: Natasha Louise de Vere

Topics: sunbird-plant pollination networks, elevational gradients, seasonality, network analysis

Skills: Pollen DNA, metabarcoding libraries, Next Generation Sequencing (Illumina Miseq), network analysis, mist-netting, R programming

LifeWebs project | Department of Ecology, Charles University in Prague, Prague, Czech Republic (2024)

Principal investigator: Robert Tropek

Topics: plant-pollinator interactions, environmental gradients, multitaxon study, metanalysis

Contribution to a global study with our dataset on sunbird-plant interactions on Mount Cameroon

SINTERVAL project | German Centre for Integrative Biodiversity research (iDiv), Leipzig, Germany (2022)

Principal investigator: Tiffany Knight

Topics: plant-pollinator interactions, elevational gradients, multitaxon study, metanalysis

Contribution to a global study with our dataset on sunbird-plant interactions on Mount Cameroon

Assessment of the conservation status of the Lion tamarins in the Atlantic Forest of Brazil | Royal Zoological of Antwerp, Antwerp, Belgium (2017)

Principal investigator: Kristel de Vleesschouwer

Topics: neotropical primates, deforestation, habitat destruction

Skills: literature review, scientific writing

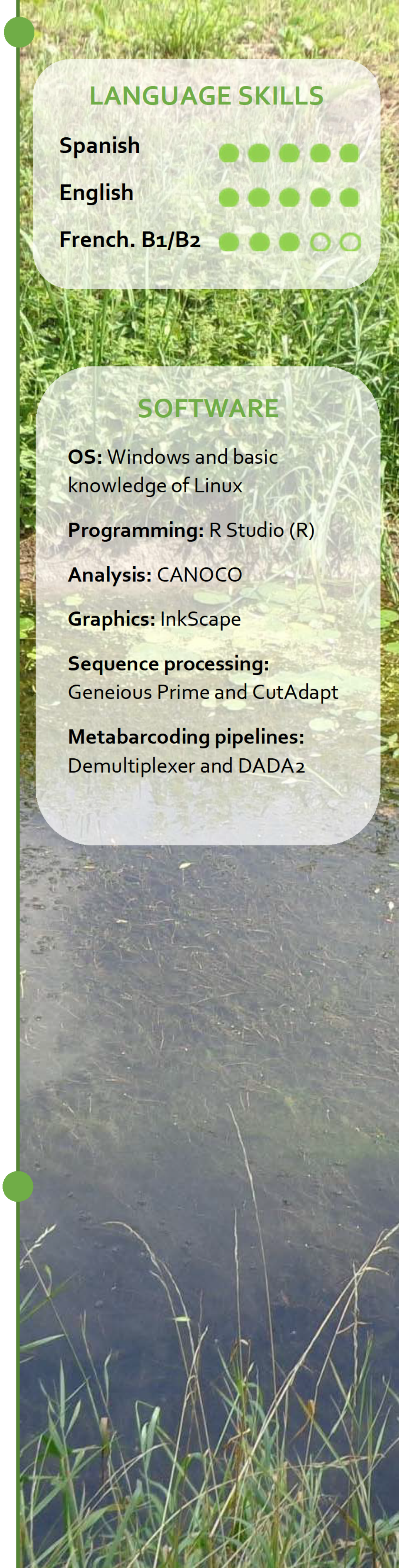
TEACHING EXPERIENCE

Advance Ecology II | Department of Ecology, Charles University in Prague, Prague, Czech Republic

Practical class for M.Sc. students of the Advance Ecology course. Metabarcoding pipeline to analyse marine biodiversity.

Molecular Methods Applied to Animal Ecology | Federal University of Paraná, Paraná, Brazil

Theoretical lecture for M.Sc. students. Use of metabarcoding for reconstructing bird-plant interactions.



LANGUAGE SKILLS

Spanish	●●●●●
English	●●●●●
French. B1/B2	●●●○○

SOFTWARE

OS: Windows and basic knowledge of Linux

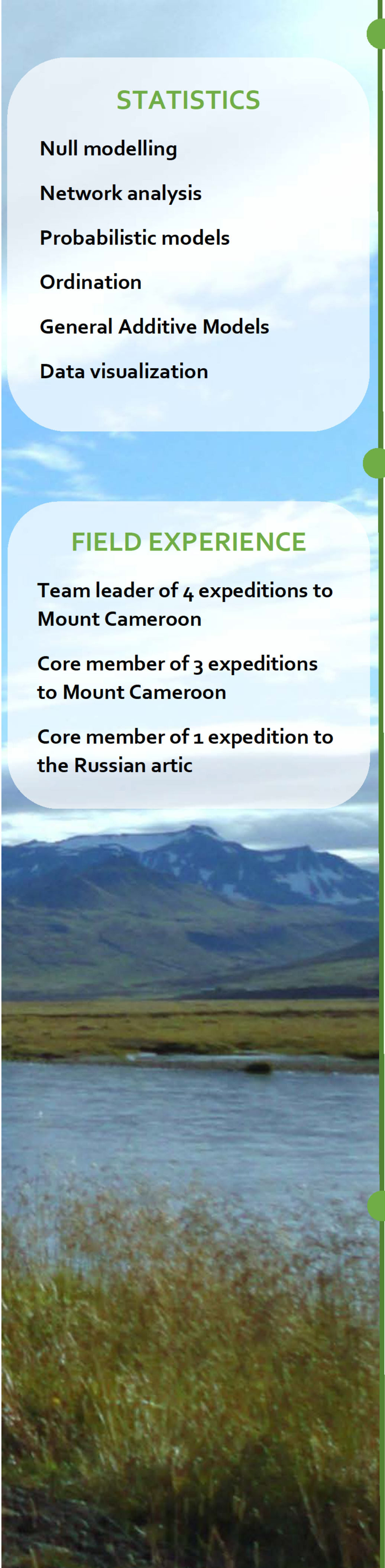
Programming: R Studio (R)

Analysis: CANOCO

Graphics: InkScape

Sequence processing: Geneious Prime and CutAdapt

Metabarcoding pipelines: Demultiplexer and DADA2



STATISTICS

Null modelling

Network analysis

Probabilistic models

Ordination

General Additive Models

Data visualization

FIELD EXPERIENCE

Team leader of 4 expeditions to Mount Cameroon

Core member of 3 expeditions to Mount Cameroon

Core member of 1 expedition to the Russian artic

GRANTS AND FUNDING

Erasmus + Mobility Programme (2024)

Four months mobility program to the lab of Natasha Louise de Vere at University of Copenhagen

Grant Agency Charles University (GAUK). Project no.: 383521 (2021-2024)

Budget: c. 900.000 CZK

Evaluation: Exceptionally good

Reconstruction of sunbird-plant pollination networks on Mount Cameroon montane grasslands, with a special focus on the main floral visitor, the Northern Double-collared sunbird (*Cinnyris reichenowi*)

CONFERENCE CONTRIBUTIONS & TALKS

Talk. Tales from Africa: Sunbird-plant interactions on Mount Cameroon | Invited speaker. Lecture series of the Department of Ecology, Paris-Lodron University, Salzburg, Austria (May 2024)

Talk. Sunbird-plant interactions on Mount Cameroon: Drivers and Ecological relationships | 4th EOU fledgelings, May 2024, Prague, Czech Republic

Talk. Coping with altitude. Pollinator shift across elevational gradients | 37th meeting of the Scandinavian Association for Pollination Ecology (SCAPE), October 2023, Namur, Belgium

Talk. Tales from Africa: Sunbird-plant interactions on Mount Cameroon | 36th meeting of the Scandinavian Association for Pollination Ecology (SCAPE), October 2022, Upsala, Sweden

Talk. Reproductive success in the Iberian lynx (*Lynx pardinus*): Effects of prey abundance, individual age and population sex-ratio | Lecture series of the doctoral program in advance environmental research, Technical University of Madrid, Madrid, Spain (November 2017)

Talk. Comparative energy budgets. The study case of the Barnacle goose (*Branta leucopis*) | Lecture series of the Animal Ecology Department, Faculty of Sciences, Utrecht University, Utrecht, The Netherlands (September 2016)

PEER-REVIEWING & CITATION METRICS

Reviewer in Journal of Plant Ecology | Oxford Academic Press. IF: 3.0, IF (5 years): 2.5. Editors in chief: Yuanhe Yang & Bernhard Schmid

Citations metrics

Google Scholar (07/2024):

46 citations, h-index: 4, i10-index: 2

ORCID: 0000-0002-0168-3080

PEER-REVIEWED PUBLICATIONS

Uceda-Gómez, G., Molua, L. L., Mani, F.T., Ewome, F.L., & Janeček, Š. [manuscript under review; Journal of Plant Ecology]. Coping with altitude: Altitude-driven visitor shifts on *Hypericum revolutum* on Mount Cameroon grasslands

Janeček, Š., **Uceda-Gómez, G.,** Janečková, P. Tropek, R., Fominka, N.T., Njie, M.M., Mlíkovský, J., Mekuate Kamga, S., Molua, L.L. & Ewome, F.L. (2024). Food resource partitioning between males and females of Volcano Sunbird (*Cinnyris preussi*) on Mount Cameroon. *Journal of Ornithology*, . https://doi.org/10.1007/s10336-024-02187-8

Uceda-Gómez, G., Chmel, K., Janečková, P., Mlíkovský, J., Klomberg, Y., Ewome, F. L., Molua, L. L., Njie, M. M., Tropek, R., & Janeček, Š. (2024). Drivers of sunbird-plant interactions on Mount Cameroon: Between neutrality and niche-based processes. *Biotropica*, 56, 136–148. https://doi.org/10.1111/btp.13290

Mekuate Kamga, S., Tamungang, S.A., Awa, T., II, Chmel, K.; Ewome, F.L., Molua, L.L., **Uceda-Gómez, G.**, Janeček, Š., Mlíkovský, J., Riegert, J. (2023). Changes in Bird Community Structure on Mount Cameroon Driven by Elevational and Vertical Gradients. *Diversity*, *15*, 727. https://doi.org/10.3390/d15060727

Mundi, O., Awa, T., II, Chmel, K., Ewome, F.L., **Uceda-Gómez, G.,** Janečková, P., & Janeček, Š. (2022). The ornithophily of *Impatiens sakeriana* does not guarantee a preference by sunbirds, *Biological Journal of the Linnean Society*, 137(2), 240–249. https://doi.org/10.1093/biolinnean/blac083

Janeček, Š., Chmel, K., Mlíkovský, J. **Uceda-Gómez, G.**, Janečková, P., Fominka, N.T., Njie, M.M., & Ewome, F.L. (2022). Spatiotemporal pattern of specialization of sunbird-plant networks on Mt. Cameroon. *Oecologia* 199, 885–896. https://doi.org/10.1007/s00442-022-05234-4

Mlikovsky, J., Chmel, K., & **Gomez, G.U.** (2022). First records of the Yellow-footed Honeyguide Melignomon eisentrauti from Mount Cameroon, with notes on its habits and biometry. *MALIMBUS*, 44(1), 58-61.

Chmel, K., Kamga, S.M., Awa, T., II, Ewome, F.L., **Uceda-Gómez, G.**, Hořák, D., Mlíkovský, J., Molua, L.L., Riegert, J. and Janeček, Š. (2021). Vertical stratification and seasonal changes of the avian community in Mount Cameroon lowland rainforest. African Journal of Ecology, 59, 655-666. https://doi.org/10.1111/aje.12877

Mlikovsky, J., Kamga, S. M., Chmel, K., & **Gomez, G.U.** (2021). Notes on Scarce Swifts Schoutedenapus myoptilus from Mount Cameroon. MALIMBUS, 43(2), 76-79.

Chmel, K., Ewome, F.L., **Gómez, G.U.**, Klomberg, Y., Mertens, J.E.J., Tropek, R., & Janeček, Š. (2021). Bird pollination syndrome is the plant's adaptation to ornithophily, but nectarivorous birds are not so selective. Oikos, 130, 1411-1424. https://doi.org/10.1111/oik.08052

Janeček, Š., Chmel, K., **Gómez, G.U.**, Janečková, P., Chmelová, E., Sejfová, Z., & Ewome, F.L. (2020). Ecological fitting is a sufficient driver of tight interactions between sunbirds and ornithophilous plants. *Ecology and Evolution*, 10, 1784–1793. https://doi.org/10.1002/ece3.5942

Crater lake

Pictures included in this thesis were taken by Guillermo Uceda-Gómez and Štěpán Janeček.

The artwork included in this thesis was made by Sandra García González.

Uceda-Gómez, G. (2024). Organization of Afrotropical plant-bird pollination communities: the effects of altitude and seasonality. Doctoral dissertation, Department of Ecology, Faculty of Science, Charles University, Viničná 7, 128 00 Prague, Czech Republic.