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Influence of military disturbances on communities of moths
Vliv vojenských disturbancí na společenstva nočních motýlů

Type of thesis

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Prohlášení

Prohlašuji, že jsem práci zpracoval samostatně a že jsem uvedl všechny použité zdroje a literaturu.

V Praze, 12. 12. 2024 ……..…………………….

Václav Koďousek

Abstract

Military disturbances, such as artillery shelling and the resulting fires from shell explosions during military training, are known to influence species diversity and community composition. This study examines a complex response of moth communities to a military disturbance intensity gradient in the Brdy Mountains, a former military training area in the Czech Republic. The disturbance regimes range from high-intensity zones near former artillery targets, through intermediate areas, where fire occurred only several times during decades, to long-term undisturbed habitats, which have remained largely untouched since forest clearing a century ago. Using data on moth abundances, life-history traits, and environmental characteristics, I analyzed how species diversity, community structure, and trait-environment relationships vary along this gradient.

Species diversity peaked in undisturbed plots, while in all the disturbed plots it was lower. RLQ analysis, Community Weighed Means-Redundancy analysis and Fourth-corner analysis revealed strong links between disturbance intensity and moth life-history traits. Open habitats with heath cover supported disturbance-dependent xerophilous species, while undisturbed closed plots with dense tree cover favored more hygrophilous species feeding on woody plants. Rare moth species showed a positive correlation with disturbance intensity, while also showing a negative correlation with deciduous tree cover.

My findings emphasize the importance of disturbance heterogeneity for maintaining moth species diversity and the habitats of rare moth species. Post-military landscapes like Brdy Mts. hold unique conservation value, supporting both disturbance-sensitive and disturbance-dependent heathland moth communities. Conservation efforts should focus on maintaining habitat mosaics via restoring the disturbance regime through prescribed burning or grazing, to support rare species and high species diversity in the open areas of the Brdy Mts.

Key words: military disturbance, moths, life-history traits, fire, conservation

Abstrakt

Vojenské disturbance, jako jsou dělostřelecké ostřelování a následné požáry způsobené výbuchy munice během vojenského výcviku, jsou známé tím, že ovlivňují druhovou diverzitu a složení společenstev. Tato studie zkoumá komplexní reakci společenstev nočních motýlů na gradient intenzity vojenských disturbancí v Brdské vrchovině, bývalém vojenském výcvikovém prostoru v České republice. Režim disturbancí zahrnují oblasti s vysokou intenzitou v blízkosti bývalých dělostřeleckých cílů, přes oblasti se střední úrovní disturbancí, kde hořelo jen několikrát během řady dekád až po dlouhodobě nerušená stanoviště, která zůstala prakticky nedotčená od doby odlesnění před sto lety. Pomocí dat o abundanci motýlů, životních strategiích a environmentálních charakteristikách jsem analyzoval, jak se druhová diverzita, struktura společenstev a vztahy mezi znaky a prostředím mění podél tohoto gradientu.

Druhová diverzita dosahovala maxima v nedisturbovaných plochách, zatímco ve všech disturbovaných plochách byla nižší. RLQ analýza, *Community weighed means-Redundancy* analýza (CWM-RDA) a *Fourth-corner* analýza odhalily silné vazby mezi intenzitou disturbancí a life-history znaky nočních motýlů. Otevřená stanoviště s vřesovištním pokryvem podporovala na disturbance závislé xerofilní druhy, zatímco nedisturbované uzavřené plochy s hustým stromovým porostem preferovaly více hygrofilní druhy, které se živí dřevinami. Vzácné druhy motýlů vykazovaly pozitivní korelaci s intenzitou disturbancí, ale zároveň negativní korelaci s pokryvem listnatých stromů.

Moje výsledky zdůrazňují důležitost heterogenity disturbancí pro udržení druhové diverzity nočních motýlů a stanovišť vzácných druhů. Postvojenské krajiny, jako je Brdská vrchovina, mají jedinečnou ochranářskou hodnotu, protože podporují jak na disturbance citlivá, tak na disturbance závislá společenstva vřesovištních motýlů. Ochranářská opatření by se měla zaměřit na udržování mozaiky stanovišť prostřednictvím obnovy režimu disturbancí, například řízeným vypalováním nebo pastvou, aby byla podpořena vzácná společenstva a vysoká druhová diverzita v otevřených oblastech Brdské vrchoviny.

Klíčová slova: vojenské disturbance, noční motýli, life-history znaky, oheň, ochrana přírody

Contents

Introduction

Disturbances, both natural and anthropogenic, are key drivers of ecological processes, influencing species composition, community structure, and the distribution of life-history traits (Turner, 2010). Although natural disturbances have historically shaped landscapes and biodiversity, anthropogenic disturbances have become more dominant in certain areas. In particular, military disturbances, such as those caused by artillery bombardment, can have lasting impacts on ecosystems, creating complex habitat mosaics that support diverse communities (Rhomme, 1982; Warren et al. 2007; Jentsch et al. 2009). Military training areas, both active and abandoned, highly affected by repeated disturbances over decades, provide unique opportunities to study these dynamics, while also providing contrasting long-term refugia for threatened biodiversity, which have not been affected by intensive agriculture or forestry (Warren et al. 2007).

Moths (Lepidoptera) are a highly diverse group of insects and sensitive indicators of environmental change, making them well suited for exploring the ecological effects of disturbances. Focus on their life-history traits (such as wingspan, larval feeding strategies, and defense mechanism) can reveal the underlying mechanisms of moth communities' response to different disturbance intensities, offering insights into resilience and vulnerability within these communities (Uhl et al. 2021). Additionally, understanding the relationship between species' commonness and habitats created under specific disturbance regime can help us uncover the conservation value of abandoned military training areas and find the best approach to their management (Reif et al. 2023).

This thesis examines how moth communities respond to a disturbance gradient in the Brdy Mountains, a former military training area in the Czech Republic. The disturbance gradient includes long-term intensively disturbed areas to areas left to spontaneous succession nearly without disturbances during the past century, encompassing habitats shaped by both fire and physical impacts from artillery shooting (Palivcová, 2018). By analyzing the life-history traits and rarity of moths along this gradient, the research aims to uncover patterns of moth community composition and mechanisms of the ecological consequences of long-term recovery following military disturbance.

The findings of this research have implications for biodiversity conservation and the management of post-military landscapes such as the former Brdy military training area. By linking disturbance history with life-history and rarity-based perspectives, this study contributes to a deeper understanding of how military disturbances shape moth diversity over time.

Literature review

Ecological succession, disturbance, and moth diversity

Ecological succession is the natural process by which ecosystems change and develop over time, involving shifts in the composition, structure, and function of ecological communities in response to environmental conditions (Odum 1969). It can be categorized into primary and secondary succession. Primary succession occurs on newly formed or barren habitats, such as those created by volcanic eruptions, where no prior life existed (Walker & Del Moral 2003). In contrast, secondary succession takes place after disturbances like fires, floods, or treefalls, where some life persists (Dalling 2008). Disturbance, defined as any discrete event that disrupts an ecosystem's structure, composition, or function, is a key driver of successional dynamics, altering resources, substrate availability, or the physical environment (White & Pickett 1985). Following a disturbance, pioneer species of plants and fauna initially colonize the site (Swanson et al., 2012). Over time, these are succeeded by larger plants and more complex vegetation, such as shrubs and fast-growing tree stands, which are eventually replaced by competitively dominant, slow-growing tree species, establishing a late-successional habitat that supports corresponding late-successional fauna. However, this process is highly dynamic and can be reset at any stage by a disturbance or maintained at a particular successional level through periodic disturbance regimes.

Moth communities undergo significant changes during habitat succession, with both abundance and species richness known to be increasing as succession progresses (Wölfling et al. 2019; Habel et al. 2019). These shifts are closely linked to moths' functional traits, particularly food source and microhabitat conditions for caterpillars. Early successional habitats favor xerothermophilous, forb-feeding moths, while later stages support hygrophilous moths associated with shrubs and trees (Pavlikova & Konvicka 2012; Potocký et al. 2018; Habel et al. 2019). Temperature and humidity of microhabitats play a role in niche segregation by creating varying conditions suitable for larval development of more species or by changing food availability (Checa et al. 2014). Moths feeding on woody plants typically have more generalized diets than forb specialists (Summerville et al. 2006; Seifert et al. 2023). In contrast, forb-feeding moths are often specialists, a trait driven by forbs' ephemeral nature and often qualitative chemical defenses (Dumroese & Luna 2016). Generalists are linked to the widespread availability, stability, and longevity of woody plants, which provide consistent resources across diverse habitats and geographic areas (Summerville et al. 2006).

The diversity of moth species is globally remarkable, with an estimated 160,000 species described, spanning a vast range of habitats and ecological niches (New, 2023). Moths are critical contributors to ecosystem functioning, serving as pollinators, herbivores, and prey for various predators and parasitoids. In the tropics, the moth species diversity is the highest, while in Central Europe, moth species diversity is lower, but still ecologically significant. Roughly 3,200 moth species in the Czech Republic alone (Laštůvka et al. 2023). This region hosts a rich assemblage of moth species adapted to temperate climates, with diversity patterns influenced by factors such as habitat heterogeneity, elevation gradients, and seasonal changes (Potocký et al. 2018). Forests, grasslands, and agricultural landscapes all serve as habitats for Central European moths, supporting their presence across diverse ecosystems—from coastal dunes to mountainous tundra and from dry grasslands to swamps and bogs. Because many moth species are highly sensitive to land-use changes and habitat fragmentation, they are considered as valuable indicators of environmental health and biodiversity in the region (Summerville et al. 2004; Rákosy & Schmitt, 2011; Habel et al. 2019).

The effects of disturbance on moth species diversity vary with the disturbance intensity, type of disturbance (fire, flood, trampling by animals etc.), the scale of the disturbance and the moth community attributes (Schowalter, 2012). They can have significant impacts on moth communities' thorough direct mortality or by altering vegetation and habitat structure including pushing back succession, changing resource availability for both larvae and adults, and microclimatic conditions. These changes cause shifts in community composition, with some species benefiting from increased resource heterogeneity, mostly herbivores, which are dependent on early successional plants. Meanwhile other species decline due to habitat loss or unsuitable conditions.

Species diversity is influenced by various mechanisms and factors, including disturbance. One key mechanism is the competition-colonization trade-off, where disturbances affect sites that are subsequently colonized by competitively weaker, fast-dispersing species. These colonizers occupy the sites until they are eventually outcompeted by stronger competitors. However, due to their superior dispersal abilities, the colonizers can move to newly disturbed sites (Cadotte et al., 2006). This trade-off, which depends heavily on the life-history traits of strong colonizers and strong competitors (Huston & Smith, 1987), can promote coexistence and increase diversity when species' colonization abilities inversely correlate with their competitive strengths (Chesson, 2000).

Disturbance-diversity relationships are inherently complex. The widely known Intermediate Disturbance Hypothesis (IDH) suggests that species diversity is highest at intermediate levels of disturbance (Connell, 1978). While some studies support this hypothesis, many report alternative relationships (Mackey & Currie, 2001; Fox, 2013). Mackey & Currie (2001) found that most studies reported no significant relationship between disturbance and diversity, indicating that disturbance often does not strongly influence diversity, while minority of studies reported monotonic relationship (positive or negative), hump-shaped relationship, or U-shaped relationship. This suggests a variety of diversity-disturbance relationships mainly influenced by the scale, intensity and frequency of disturbances and also the characteristics of the affected community.

Fire and physical disturbance and their effects on moth communities

Wildfire, one of the major disturbance agents, is an uncontrolled fire that spreads rapidly through vegetation-dense areas, driven by dry conditions, wind, and combustible materials, often resulting in significant ecological and environmental impacts (Thonicke et al. 2001). In contrast, controlled fires are referred to as prescribed burning (Valkó et al., 2014). Fire can result in high mortality rates among plants and animals, restart successional stages, release nutrients from burned vegetation (often removed from the site by wind and water erosion), and create opportunities for colonization while providing burned biomass as a potential resource (Wikars & Schimmel, 2001; Wikars 2002; Kouki et al., 2012). Physical disturbance encompasses physical disruptions to the environment caused by external forces, often from human or animal activities, including logging, soil plowing, and trampling by livestock. These disturbances can remove topsoil, expose bare ground and rocks, and create depressions that alter the soil surface. Unlike fire, which depletes nutrients, physical disturbance typically redistributes them unevenly and is generally less intense. Similarly to fire, it can reset successional stages and facilitate the colonization of early successional flora and fauna.

Effects of physical disturbance on moths vary, especially based on the type of disturbance, which habitat and moth community it affects and with the disturbance intensity.

Fires can be characterized by their severity, intensity, spread, frequency, timing and the vegetation levels they affect (Lentile et al. 2006; Keeley 2009). These characteristics are interrelated and influence one another. For my thesis, fire and burn intensity, fire frequency and fire intensity are especially important.

Fire severity typically describes the immediate post-fire condition of vegetation and soil, whereas burn severity refers to the time required for the ecosystem to recover its functions (Keeley 2009). Burn severity is often higher in late-successional habitats if fire severity is high, while early successional habitats may experience low burn severity even after a high-severity fire.

Fire intensity measures the energy released and the rate of spread, influenced primarily by fuel type and condition, as well as weather factors like rainfall, wind speed, and direction (Hargrove et al. 2000; Keeley 2009). High-intensity fires generally cause greater destruction and higher mortality among plants and animals. Fire dynamics often vary during an event, with intensity and severity differing across areas, resulting in heterogeneous effects on the landscape. In heathlands like those in Brdy Mts., fire intensity is highly influenced by current conditions and tends to increase after prolonged fire-free periods due to fuel accumulation. Fire severity also rises with longer intervals between fires, reflecting greater immediate impacts on vegetation. However, burn severity, which indicates longer-term ecosystem effects, is less affected due to the resilience of fire-adapted plant assemblages. While burn severity may increase gradually over time, it generally remains moderate even after extended fire-free periods.

The timing of a fire plays a crucial role in its ecological impact. Timing is particularly crucial as it influences the direct impact of fire on moths, as well as on animals and plants in general. While fires can occur year-round, most wildfires in Europe happen during the summer, whereas in Brdy Mts., they predominantly occur in late spring (Sedláček et al. 2015). However, these numbers are heavily influenced by wildfires in southern Europe, where about 90 % of European fires occur (European Commission 2018).

The direct effects of fire on moths are straightforward. Fire causes moth mortality through heat and burning, with non-adult stages (eggs, larvae, and pupae) being the most vulnerable, particularly those inhabiting forbs and grasses. Moths residing in tree crowns have a higher chance of survival, unless the fire escalates into a crown fire (Kral et al. 2017). Larvae and pupae hidden underground may also survive, as can individuals that find refugia, for example in unburned patches or between rocks (Gongalsky & Persson, 2013; Thom et al. 2015). Highly mobile adult moths are the most likely to survive and are also capable of rapid colonization, depending on the species' dispersion ability (Gustafson et al. 2019; Moyo, 2022).

Indirect effects of fire on moths primarily involve habitat modification and changes in the availability of food plants. The colonization or re-establishment of plant species depends largely on the size of the burned area and the severity of the fire. In smaller, less severely burned areas, colonization occurs quickly, with surrounding vegetation recovering within a few years (Viedma et al. 1997). In larger, more severely burned sites, the process follows a different trajectory. Immediately after the fire, anthracophilous and pyrophilous species of fungi and plants colonize the site. Some of these species are food sources for dietary specialists, such as the snout moth *Apomyelois bistriatella* (Pyralidae), which feeds on the pyrophilous fungus *Daldinia vernicosa* (Xylariaceae), and has been observed in burned habitats (Wikars 1992, 2002). Other species can be attracted by smoke like *Actebia fennica* (Noctuidae), which feeds on early successional herbs (Everaerts et al. 2000).

The immediate effects of fire disturbance on moth communities have been studied more extensively than those of military disturbance, with research conducted in Asia (Bae et al. 2011; Choi 2018), North America (Chaundy-Smart et al. 2012; Schaeffer 2013; Guerra et al. 2019; Brantley et al. 2023), and Africa (Axmacher et al. 2019). However, European studies are limited, with only two studies to date and my knowledge (Banza et al. 2019; Walter et al. 2022). The two European studies, conducted in the Mediterranean and Central Europe, shared a key finding: both described declines in moth abundance and species richness after fire, likely due to high mortality (Banza et al. 2019; Walter et al. 2022). In the Mediterranean, this decline occurred despite an increase in flowering plant abundance (Banza et al. 2019). In contrast, in Central Europe, species richness was lower at the burned site compared to unburned sites, but species diversity was higher due to the homogeneity of the surrounding area and the arrival of xerophilous species (Walter et al. 2022). Additionally, Banza et al. (2019) found that moths transported pollen from 83% of locally flowering plants, but the robustness of the pollen transport network decreased after fire, emphasizing the disruption of mutualistic relationships. While these two studies were limited in scope and offer little direct comparison, they highlight a gap in research on the effects of fire on moth communities in European temperate habitats.

From the studies outside Europe, two consistent patterns emerge: first, moth abundance and species richness typically decrease shortly after fire (Bae et al. 2011; Schaeffer 2013; Choi 2018; Walter et al. 2022; Brantley et al. 2023); second, moth species composition on burned sites is closely linked to the availability of host plants (Chaundy-Smart et al. 2012; Schaeffer 2013; Choi 2018; Banza et al. 2019; Guerra et al. 2019; Walter et al. 2022; Brantley et al. 2023). Interestingly, moth abundance increased after a low-intensity prescribed fire, likely due to an increase in forb cover (Guerra et al. 2019). Choi (2018) also showed that moth communities can recover within a few years, with species occurrence tracking the recovery of their host plants (Bae et al. 2011). A notable difference between studies was the decrease in moth diversity observed by Bae et al. (2011), in contrast to Walter et al. (2022), which may be attributed to differences in habitat heterogeneity, which influenced moth diversity in unburned areas.

Over the months following the fire disturbance, fire-favoring pioneer plants colonized the site. These plants are adapted to rapidly colonize burned areas, either by germinating or flowering in response to heat or smoke exposure, or by surviving fires through traits such as thick bark or underground structures that allow regrowth (Keeley et al. 2011). In Central Europe, fire-favored species are rarer than in fire-prone regions like Southern Europe, but examples include bracken (*Pteridium aquilinum*), heath (*Calluna vulgaris*), and European white birch (*Betula pendula*), which all are key colonizers of burned areas in the Brdy region (Palivcová 2018; AOPK ČR, 2023). Moths whose larvae feed on these species may benefit from fire disturbances for years, and potentially over a decade, following a fire (Bae et al. 2011). After two or more decades, the disturbed site begins to favor shrub and tree-feeding moth species, and the effects of the original fire disturbance diminish (Wölfling et al. 2019; Habel et al. 2019)

Military disturbance and biodiversity

Military training areas (MTAs) serve as designated areas for national defense and armed forces training. These areas are used for exercises, combat simulations, and equipment testing in realistic environments, often involving live fire and vehicle movement. In Czechoslovakia areas for military activity were established in dozens smaller locations, but only after the start of Cold war in the 1950s were 12 large MTAs created, 8 of which were in the region of current Czech Republic (MO ČR, 2024; VLS ČR, 2024). Due to downsizing of the army after the end of the Cold War in the 1990s (Tagarev, 2004), many MTAs started to be abandoned and in the Czech Republic only 4 active MTAs remain, covering a total of 83,127 ha (~1.05% of the Czech Republic's area; MO ČR, 2024).

MTAs are typically characterized by a unique set of anthropogenic disturbances. These include physical disturbances from armored vehicles and foot soldiers, as well as fire disturbances caused from explosions of various hand weapons and artillery shelling (Demarais et al. 1999). Armored vehicles disturb or even remove the topsoil and vegetation, often forming ephemeral puddles when combined with rain. Fire disturbances temporarily increase nutrient availability but lead to long-term nutrient depletion. Explosions also create terrain depressions, exposing rocks and boulders. Unlike the uniform impacts of most modern human activities, military disturbances generate a heterogeneous mosaic of habitats at varying disturbance intensities and successional stages, which enhances biodiversity (Warren et al. 2007). The scale, intensity, and timing of these disturbances vary widely, contributing to their habitat complexity (Warren et al. 2007). Military disturbances are also accompanied by various negative consequences, including oil spills, increased erosion, unexploded ammunition, and contamination with toxic substances (Demarais et al., 1999; Broomandi et al., 2020).

In recent decades, military training areas (MTAs) have attracted significant conservation interest. Their long-term exclusion from intensive agriculture and forestry (including overuse of fertilizers and biocides), combined with their unique disturbance regimes, has created valuable habitats for numerous rare species and habitats, most notably low-nutrient grasslands, heathlands and sand dunes (Ellwanger & Reiter, 2019). Additionally, undisturbed sections of MTAs have served as refugia for species reliant on stable habitats, unaffected intensively managed surrounding landscapes (Bušek & Reif, 2017; Harabiš & Dolný, 2018).

Among vertebrates, it has been found out that certain communities benefit more from military disturbances than others. Bušek & Reif (2017) and Culmsee et al. (2021) analyzed bird communities and species composition across large areas of abandoned military training areas (MTAs) in Czechia and Germany, respectively. Their findings revealed that MTAs support bird communities of high species richness and conservation value, particularly those associated with open and semi-open habitats. Building on these results, Dvořáková et al. (2024) examined shifts in bird community composition in abandoned Czech MTAs. They observed declines in open-habitat species alongside increases in forest-associated species. However, species targeted by specific management efforts remained stable, underscoring the importance of active habitat management to preserve these valuable areas. Similarly, Warren & Büttner (2008a) demonstrated strong disturbance-dependence in two endangered amphibians (*Bufo calamita* and *Bombina variegata*) in German MTAs. These species preferred recently disturbed (<2 years) pools with high bare ground cover and minimal vegetation, while more common frog and newt species either showed no preference for disturbance or favored less disturbed areas. Voska (2018) investigated reptile diversity in the Brdy Mts. Mountains, an abandoned Czech MTA, and found high species richness in intensively disturbed areas such as Jordán and Tok. This was likely due to the habitat heterogeneity created by past military activity. Collectively, these studies emphasize the critical need to maintain disturbance regimes in abandoned MTAs or implement alternative management strategies to replicate military disturbances. Preserving open habitats and semi-open habitat mosaics is essential, as they host the highest species diversity and numerous species of conservation concern.

Invertebrates, like vertebrates, exhibit strong associations with military training areas (MTAs). While butterflies and beetles are the most frequently studied groups in MTAs (Caudal & Gallet 2023), moth-related research remains limited. For this reason, I chose to discuss butterflies and moths both together and separately from other invertebrate groups. To my knowledge, the only study examining multiple arthropod groups was conducted by Palivcová (2018) in a former MTA in Brdy Mts. (Czech Republic), where she explored the effects of military disturbances along an intensity gradient. Her results revealed that Aculeata (Hymenoptera) had significantly higher abundance and species richness in more intensively disturbed areas, whereas spiders, beetles, and orthopterans showed no clear response to the disturbance gradient.

Several studies have examined the effects of military disturbances on specific insect groups or populations. For instance, Harabiš & Dolný (2018) and Šíblová et al. (2021) investigated the impacts of military activities on dragonflies in Czech and Slovak MTAs, respectively. Both studies reported similar or even higher species richness within MTAs compared to surrounding landscapes. Interestingly, while dragonflies preferred undisturbed refugia within MTAs and were not directly reliant on disturbance, military activities indirectly supported their diversity by preserving habitat isolation from intensive land use. In the USA, Graham et al. (2009) explored ant diversity and abundance along a disturbance intensity gradient at Fort Benning. They observed that species richness peaked at intermediate disturbance levels (43% relative disturbance), forming a hump-shaped disturbance-diversity relationship (DDR). Ant abundance, on the other hand, was highest at higher disturbance levels (85%). The increased species richness at intermediate disturbance was attributed to enhanced habitat heterogeneity.

Species-specific studies further highlight the role of military disturbances in supporting rare and disturbance-dependent species. For example, Warren & Büttner (2008b) examined populations of the rare grasshopper *Oedipoda caerulescens* and the beetle *Cicindela hybrida* in four active MTAs in Germany. They found that *O. caerulescens* preferred areas with 60–100% surface disturbance and 50–70% plant cover, while *C. hybrida* thrived in areas with >40% surface disturbance and approximately 60% plant cover. Drag et al. (2011) studied the metapopulation dynamics of the beetle *Rosalia alpina* in the former Ralsko MTA (Czech Republic). *R. alpina* benefited from the lack of intensive forestry in active MTAs, persisting in refugia on old beech-covered hilltops. These populations were highly connected, with adults traveling up to 1.6 km, and reached densities of 42–84 individuals per hectare annually.

Additionally, military disturbances have been shown to favor puddle-dwelling crustaceans, such as *Branchipus schaefferi*, which frequently inhabit areas disturbed by military vehicles, including tank tracks (Merta & Roleček, 2005; Gołdyn et al., 2007; Schernhammer et al., 2020). However, comprehensive studies on the effects of military disturbances on this group remain limited.

These findings emphasize the ecological importance of MTAs in maintaining habitat heterogeneity, supporting rare and disturbance-dependent species, while also conserving untouched refugia. To sustain these unique communities, it is essential to continue disturbance regimes akin to those caused by military activities while protecting refugia from threats like renewed forestry operations and habitat transformation for agriculture or housing.

Effect of military disturbance on lepidopteran communities

Several studies on effects of military disturbance on lepidopteran communities have been performed. While some only focused on moth species diversity in MTAs (Walczak 2011; Nowacki & Pałka 2015; Ferster et al. 2008), some made comprehensive studies on large groups of butterflies and/or moths (Cizek et al. 2013; Palivcová, 2018; Reif et al. 2023) and Zografou et al. (2017) focused on a single butterfly species. Konvicka et al. (2011) also focused on potential management renewal effects on butterfly community.

Walczak (2011) and Nowacki & Pałka (2015) conducted faunistic research in Polish MTAs focusing on moths. Walczak (2011) surveyed leaf-mining Microlepidoptera in Poland's Biedrusko military area, recording 258 species across 20 families. The relatively high species diversity was attributed to habitat heterogeneity and rich plant species diversity. Similarly, Nowacki & Pałka (2015) studied Noctuoidea moths in the Nowa Dęba MTA, identifying 273 species (55% of Polish Noctuoidea), including rare and endangered hygrophilous, psammophilous, and xerothermic species for which the MTA serves as a refugium. Ferster et al. (2008) also conducted faunistic research to find if the Fort Indiantown Gap National Guard Training Area (USA) harbors a Lepidoptera community of conservation value. They identified 237 moth species, including several species of conservation interest, with some species of great conservation value, realizing that the site serves as a refuge for grassland species, which require periodic disturbances. In the Czech Republic Cizek et al. (2013) studied butterfly and plant diversity in 41 abandoned Czech MTAs, which they compared to 125 nature reserves. They found that plant species richness was comparable to the species richness of nature reserves, while they found higher butterfly richness in MTAs but fewer endangered species, which were predominantly disturbance dependent. Overall, it can be said that abandoned MTAs have the potential to host a significant number of moth and butterfly species, which are often uncommon or rare in the surrounding area.

Several studies have examined the effects of military disturbances on moth and butterfly communities. Palivcová (2018) investigated the impact of disturbance intensity on selected arthropod groups, including moths, in the Brdy PLA. Moth abundance and species richness were highest in minimally disturbed plots, whereas butterflies showed no significant variation in abundance or species richness across disturbance levels. While no clear differences in moth conservation value were observed along the disturbance gradient, deciduous tree cover was found to ambiguously influence moth community composition. Kim et al. (2015) only focused on butterfly communities in South Korea by comparing an active MTA, a secondary forest, and an old-growth forest. The MTA had the highest species richness (82 species) and supported the largest number of Red-Listed species (13), including grassland species absent from the other sites. These findings highlight the critical role of MTAs in conserving grassland and other open-habitat species, emphasizing the importance of targeted management to maintain such habitats. The importance of MTAs grassland was also highlighted in study by Zografou et al. (2017), who found a strong dependence on military disturbance in their target species, butterfly *Speyeria idalia idalia* (Nymphalidae). They studied the long-term effects of management (logging and prescribed burning) on the population of extremely rare grassland butterfly *Speyeria idalia idalia* in active Fort Indiantown Gap National Guard Training Area (USA) and found out that the species thrived in areas widely affected by logging and prescribed burning.

Reif et al. (2023) and Konvicka et al. (2011) focused on management of abandoned MTAs. Reif et al. (2023) examined how different management approaches impact biodiversity changes in vascular plants, grasshoppers, butterflies, and birds in abandoned MTAs. They found vascular plants and grasshoppers showed positive biodiversity changes over time, while butterflies experienced negative changes, with beta-diversity driven by common species loss and birds displayed mixed responses. The responses of different groups to management types varied significantly. Woody plant cutting was found to be beneficial for plants and grasshoppers. Grazing for conservation supported plants and birds, but it had a negative effect on butterflies. Grazing for agriculture had similar mixed impacts. Mowing for conservation was linked to negative changes in plants and vehicle movement had negative impact on butterflies. Overall butterflies did not benefit from abandonment of MTAs and neither did they respond positively to any type of management. As a potential conservation tool for butterfly protection seems to be grazing by large ungulates as shown by Konvička et al. (2021). Konvička et al. (2021) studied the impact of large ungulate rewilding on butterfly communities in a former military training range in Milovice (Czech Republic). They found that butterfly species richness decreased after the cessation of military use in the 1990s due to successional changes, especially due to the disappearance of early successional species. Rewilded plots grazed by Exmoor ponies, Tauros cattle, and European wisents supported higher butterfly species richness and abundances compared to neglected plots. Smaller-bodied butterflies, which rely on small, competitively poor plants, thrived in the rewilded areas, while larger-bodied butterflies associated with coarse grasses and shrubs were more abundant in the neglected plots. Large ungulate grazing thus seems like a useful conservation tool in former MTAs and could be applied in some neglected MTAs. Based on findings from other research, it can be anticipated that rare and endangered moth species, particularly those that feed on fire-adapted plants, would be the primary conservation focus. Prescribed burning, which is most often applied to heathlands and dry grasslands, habitats of significant conservation value for moths (Fielding 1992), has the potential to support these species (Konvička et al. 2005; Pešout 2021).

The recent abandonment of many MTAs has raised conservation concerns, as the absence of disturbance can lead to overgrowth of open habitats by shrubs and trees, threatening their ecological value (Jentsch et al. 2009; Jirku et al. 2020). To address this, many MTAs have been formally protected under the NATURA 2000 network. In the Czech Republic, several MTAs have been designated as Special Areas of Conservation (SACs), including Hradiště, Boletice, Libavá, Milovice–Mladá, and smaller sites like SAC Tok (AOPK 2024a). Many of these areas are also protected as part of national conservation initiatives, such as the Protected Landscape Area Brdy Mts. While the protection areas have been established, there are still issues, due to lack of management and reluctance to use prescribed burning (Pešout, 2021).

Aims and hypotheses

Based on the literature review, I propose the following aims and associated hypotheses for my thesis:

1. To investigate how moth species diversity varies along a gradient of disturbance frequency:
    - Moth species richness and diversity will increase as disturbance intensity decreases.
2. To explore how environmental gradients associated with military disturbance influence the relationship between moth species composition and their functional traits, and to identify key life-history traits of moth species under varying environmental conditions:
    - Moths that prefer dry, warm, and open habitats will show a significant positive association with intensively disturbed areas.
    - Moths that prefer humid, cool, and closed habitats will show a significant positive association with minimally disturbed areas.
    - Dietary generalist moth species will exhibit a strong association with the least disturbed habitats.
    - Moths with a spring flight period will be positively correlated with disturbance intensity.
3. To analyze the relationships between specific life-history traits and environmental characteristics:
    - Tree-feeding moths will show a significant positive relationship with tree cover and disturbance intensity, while forb-feeding moths will exhibit the opposite trend.
    - Moth species with hairy larvae will display a significant negative relationship with both vegetation cover and tree cover.
4. To explore potential connections between species rarity and disturbance intensity:
    - Moth species' commonness will show a significant negative correlation with disturbance intensity.
5. To propose conservation strategies to support moth communities in the Jordán and Tok artillery ranges, with a particular focus on rare species and species diversity.

Materials and methods

In this thesis, I have processed datasets collected by other researchers for a master thesis of Lucie Palivcová focused on the Influence of military disturbances on species richness and conservation value of arthropod communities in Brdy Mts. (Palivcová, 2018). I have processed and analyzed them with original approaches and methods, and in combination with other published datasets (Potocký et al. 2018), to meet the abovementioned original aims.

Study area and design

The study area is situated in the former military training grounds of the Brdy Mts. Mountains, located in Central Bohemia. The Brdy Mts. Mountains form the core of the inland *Oreophyticum* (Slavík, 1988), one of the few tall mountain ranges in the Czech Republic that are not located along its borders (Balatka & Kalvoda, 2006). As such, they serve as both a natural barrier for lowland species and a refugium for mountain species, while also being influenced by the surrounding species pool of lowland species. The region is characterized by extensive woodlands, predominantly spruce and mixed forests, interspersed with peat bogs, heathlands, meadows, and rocky outcrops (AOPK ČR, 2016).

Brdy Mts. features 10 peaks exceeding 800 meters above sea level, with Tok being the highest at 862 meters. The highest elevations experience an average annual temperature of around 5.5 °C and precipitation reaching up to 800 mm, contrasting with nearby lowland areas. For instance, the town of Příbram records an annual average temperature of 7.3 °C and 623 mm of precipitation, while Rokycany experiences slightly warmer temperatures at 8.0 °C but higher precipitation at 843 mm. These differences highlight the notably colder and wetter conditions in the upper parts of Brdy Mts (AOPK ČR, 2024c).

The central Brdy Mts. region was designated an artillery range by the Czechoslovak government in 1926 (Benedikt, 2014), with artillery target ranges Jordán, Tok, and Brda established between 1928 and 1931 (Sedláček & Marhoul, 2016). In the following years, the range expanded, and on 1st July 1950, it was officially reclassified as a military training area (Benedikt, 2014). Further expansion occurred in 1952, and this boundary remained unchanged until 2016, when the military zone was significantly reduced to the Jince Garrison Training Area, which still includes the Brda target range (excluded from this thesis). The larger part of the previous MTA was designated as the Brdy Landscape Protected Area (CHKO Brdy Mts.; Hubl, 2019).

Jordán and Tok artillery ranges are situated in the central part of Brdy Mts., above 800 meters. The climate in the artillery ranges is defined by relatively short, cool, and humid summers, followed by relatively long, mild to wet winters with prolonged snow cover. The substratum in these areas is composed of extremely poor and hard quartz conglomerates, further shaping the region's ecological characteristics (AOPK ČR, 2023)

Three major types of disturbances have shaped the ecosystems in Tok and Jordán. The first was deforestation by the military a century ago in the 1920s, which opened the landscape and allowed open-habitat species to colonize. In peripheral and remote areas, spontaneous vegetation succession eventually reached a stage of mature deciduous, coniferous, or mixed forest stands, and it persisted fairly unchanged until today. Two other types of disturbances have recurred annually, usually even several times a year: physical impacts from artillery shells and the resulting fires. The impact of artillery creates depressions edged with rocks and bare soil, often filling with rainwater. Deeper craters support organic matter accumulation and the colonization by peat vegetation, together with an initiation of the peat formation processes. Bombardment also frequently ignites fires, which play a critical role in delaying succession, creating open spaces for fire-adapted plants and moths that rely on them (Midgley & Bond 2013). Among the most important fire-favored plants are heath (*Calluna vulgaris*), bracken (*Pteridium aquilinum*), and European blueberry (*Vaccinium myrtillus*) (Palivcová, 2018). Palivcová (2018) also found distinct differences in successional processes on Jordán and Tok, noting that Jordán has been affected by an encroachment of European white birch (*Betula pendula*), which accelerated local succession. Frequent fires and physical disturbances in heavily used areas created extensive open heathlands, interspersed with small, fragmented bogs, with diverse gradients between them and mature forest stands (Pešout, 2016).

Fires on Tok have been generally more frequent and extensive than on Jordán (VHJ Jince, 2015; Sedláček et al. 2015), often recurring in the same areas and with similar intensity (Palivcová, 2018). Artillery target placement influenced fire hotspots and frequent artillery bombardment lead to an overabundance of smaller fires and fewer large ones. For instance, between 2006 and 2015 Tok experienced seven fires exceeding 1 ha, one fire between 5 and

10 ha, and six fires larger than 10 ha, two of which spanned around 100 ha (VHJ Jince, 2015). In Jordán, eight fires exceeded 1 ha, and one surpassed 10 ha (VHJ Jince, 2015). Numerous smaller fires were documented, likely with numerous additional undocumented smaller-scaled incidents.

Study design

Palivcová (2018) selected the plots based on analysis of map documents and records of fire disturbances over the ten years preceding the study. A total of 24 plots were chosen (12 on each artillery target range) and grouped into three categories based on similar environmental characteristics (pseudoreplications) to ensure comprehensive representation (Palivcová, pers. comm.). Each group contained four plots with varying disturbance intensities: High disturbance (I) intensity was located near the artillery targets and experienced most intense disturbances. Medium disturbance intensity (II) and low disturbance intensity (III) were placed further away from artillery targets and experienced gradually less frequent and less intense disturbances. Very low disturbance intensity (IV) was placed on the periphery of target ranges and had experienced no military disturbance over the past century. Thus, they formed three blocks of four plots on different intensity disturbance levels. Plot spacing ranged from 15 to 200 meters, and each plot measured 25 meters in diameter (see Fig. 1).

Data sampling

Data was collected by portable light traps to capture moths. Once a month during the study period (May 16–17, June 19–20, July 17–18, and August 14–15), light traps were set in the plots overnight and emptied the following morning. Identification was then conducted by Pavel Potocký and Lucie Palivcová (Palivcová 2018).

Each plot was characterized by a set of habitat characteristics (Palivcová 2018). Every habitat characteristic was expressed as surface coverage and visually calculated while visiting the plots in July. All measured habitat characteristics (environmental variables) were vegetation cover (VEGCOV), bare ground (BARGRD), bare rocks (ROCKS), and various vegetation strata—E0 (moss), E1 (forb, <1 m), E2 (shrub, 1–5 m), and E3 (tree, >5 m), wetland vegetation (WETVEG), heath (HEATH), blueberry (VACCIN), grass (GRASS), bracken (BRACKN), dense (DENVEG) or sparse vegetation, tree cover, deciduous (DECTRE) and coniferous cover (CONTRE), and dead plant matter (DEPLMA). These variables were selected for their relevance in describing environmental conditions for the studied arthropod groups, while they were also easily visually identifiable in the field (Palivcová, pers. comm.). For a complete list and description of environmental variables, see Table 1.

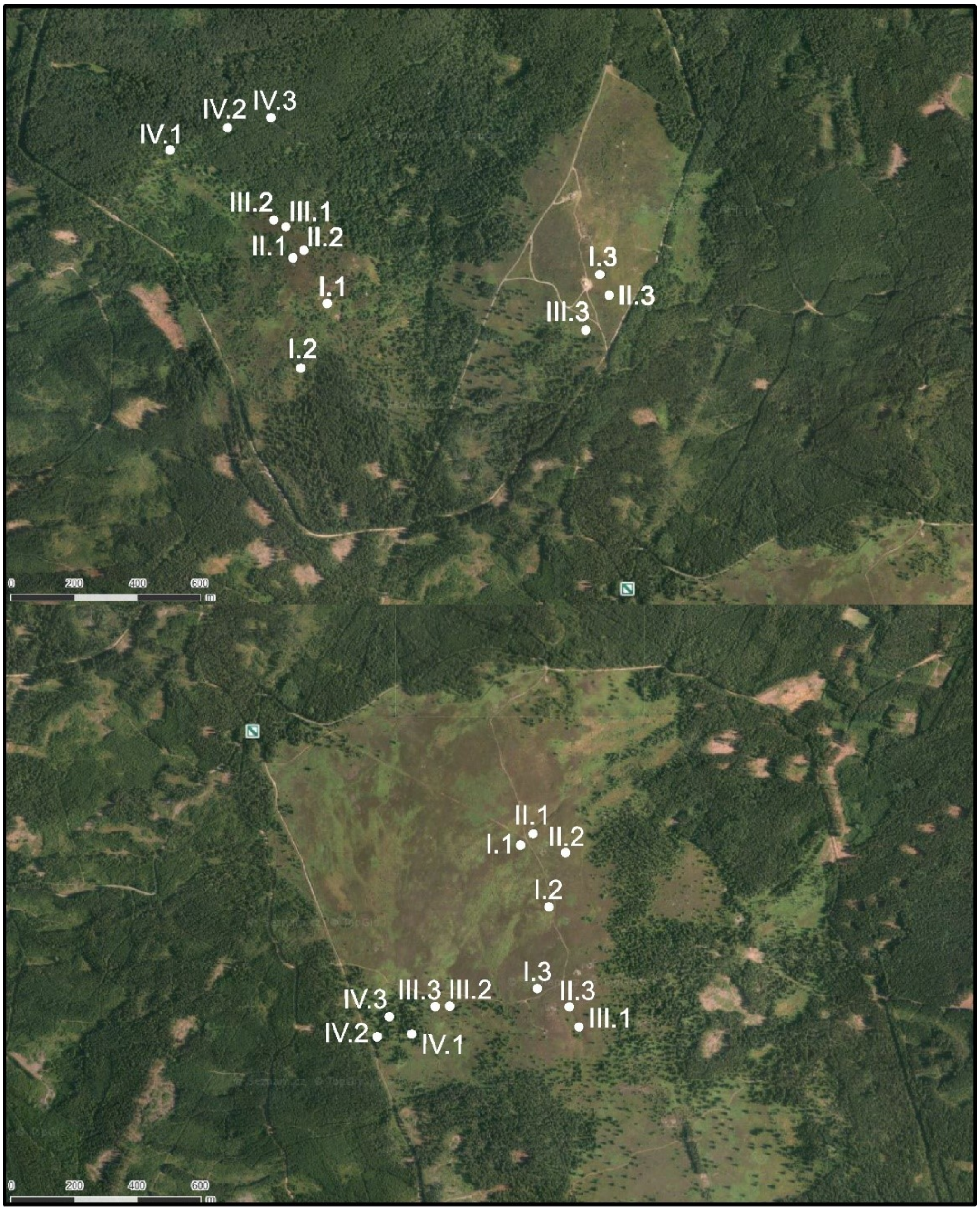


Figure 1 – Map of Jordán (top) and Tok (bottom) artillery ranges with marked plots. Roman numerals indicate disturbance intensity (IV = very low, III = low, II = medium, I = high), while numbers specify individual plot category.

Palivcová (2018) collected a total of 10,827 individuals representing 196 moth species across eight families: Geometridae, Noctuidae, Erebidae, Drepanidae, Hepialidae, Lasiocampidae, Notodontidae, and Sphingidae. Among these, only eight species were included in the Czech Republic's Red List of Threatened Species (Hejda, 2017). The most abundant species were *Lycophotia porphyrea*, with 3,778 individuals (34.89%), *Eulithis populata*, with 1,773 individuals (16.38%), and *Pachycnemia hippocastanaria*, with 943 individuals (8.71%). Following data modification for analyses (see further), 120 species remained: 61 from Geometridae, 38 from Noctuidae, 12 from Erebidae, 4 from Drepanidae, 3 from Notodontidae, 1 from Hepialidae, and 1 from Lasiocampidae.

Figure 2 – Photographs of sites from Tok artillery range affected by different levels of disturbance intensity. In the top left is a site disturbed with high intensity (I.), top right is a site disturbed with medium intensity (II.), bottom left is a site disturbed with low intensity (III.) and bottom right is a site disturbed with very low intensity (IV.).

Moth life-history traits

I used a dataset compiled by Potocký et al. (2018) for lepidopteran life-history trait data. This dataset was selected for its Central European focus, offering regionally accurate information on moth life-history traits. They were represented by a wide range of different traits focused on mobility and generation cycle traits (6 traits), traits related to flight period (6 traits), larval feeding traits (7 traits), defense mechanisms/behavior (6 traits), traits related to adult activity and resource use (2 traits), traits related to habitat use (18 traits), and traits related to species range (2 traits). For a complete list and description of life-history traits, see Table 2.

Besides the traits listed in Potocký et al. (2018), I included three additional life-history traits. The first, commonness (COMM), quantified the distribution of each species in the Czech Republic. To calculate it, I utilized the Species Occurrence Database (AOPK ČR, 2024), which compiles distribution data for all species, including moths, across the Czech Republic. The distribution map is based on faunistic grid squares measuring 12x11 km, covering the country with a total of 628 squares. Data can be categorized based on the time of observation, with older records often being less complete than more recent ones, which more accurately reflect the current state of the landscape. Therefore, I focused only on data collected after 2010, for each species recorded by Palivcová (2018).

The other two additional traits were coloration of caterpillars and coloration of adults, with a particular focus on aposematic coloration. I categorized the selected species using visual representations from Macek et al. (2007, 2009, and 2012). Larvae were divided into two categories based on the presence of aposematic coloration, while adults were sorted into three categories: first category contained adults exhibiting aposematic coloration, second category contained species with cryptic coloration and with the third category consisting of adults exhibiting aposematic coloration on their hindwings. Unfortunately, both traits showed minimal variation, as nearly all selected species displayed cryptic coloration, leading to their exclusion from the analyses as described further.

Statistical analyses

First, I characterized moth species diversity and examined whether species diversity significantly differed across disturbance intensity levels. To assess species richness and evenness along the disturbance gradient, I calculated Shannon's diversity index (H'), Simpson's diversity index (λ), and the Chao1 index using the diversity function for the first two indices and the estimateR function for the Chao1 index from the *vegan* package (Oksanen et al., 2013) in R. These selected indices differ in their approach and thus they can comprehensively describe species diversity on the sites. Shannon Index measures diversity, accounting for both species' richness (number of species) and evenness (relative abundance). It gives more weight to rare species than the Simpson Index, making it sensitive to changes in less abundant species. Simpson Index (1-D) emphasizes the dominance of common species over rare ones. It is less sensitive to rare species and reflects the probability that two randomly selected individuals belong to the same species. Chao1 Index estimates species richness, focusing on the total number of species in a community, including undetected ones. It uses the number of rare species (e.g., singletons and doubletons) to predict the true species richness. Higher values of all the used indices indicate greater diversity.

To test for statistically significant differences in species diversity across disturbance intensity levels, I used Generalized Estimating Equations (GEE) with the *geepack* package (Højsgaard et al. 2024) in R. GEE accounts for within-group correlations (pseudoreplications), and thus the block design, using the grouping variable *id*. A Gaussian distribution was applied because species richness and diversity are continuous variables and did not significantly deviate from a normal distribution as tested by Shapiro-Wilk test. An exchangeable correlation structure (corstr = "*exchangeable*") was chosen, assuming equal correlation within groups. After that I used Analysis of variance (ANOVA) on the resulting model, which tests the null hypothesis that all disturbance intensity levels of have the same effect on species richness ($p>0.05$). Pairwise differences between disturbance levels were assessed using estimated marginal means (EMMs) from the *emmeans* package (Lenth, 2024), with Bonferroni correction applied for multiple comparisons.

To analyze the relationships between moth life-history traits and disturbance intensity, I applied the RLQ analytical approaches (Legendre et al. 1997; Dray et al. 2014). After compiling all the data, I obtained three main tables: R, L, and Q. Table R (environmental characteristics) contained plots as rows and environmental variables as columns. Table L (abundance) included plots in rows and species abundances in columns. Table Q (life-history traits) listed moth species in rows and their corresponding life-history trait states in columns. Prior to further analyses, I made several adjustments to tables L, R, and Q to ensure robust results and proper functioning of the analyses.

Table L (moth abundance table):

I removed singletons (species with one occurrence per plot) to minimize random observations unrelated to species' habitat use, reducing the number of species from 194 to 120. To address skewness and reduce the influence of outliers, I applied a logarithmic transformation ($\log(X+1)$) to the abundance data.

Table Q (moth life-history trait table):

Underrepresented life-history traits were excluded to avoid weak or unreliable associations, such as traits present in only a few species (e.g., wingless females, represented by 3 species). Similarly, overrepresented traits (e.g., summer flying period, present in 111 species) were also excluded. This adjustment reduced the number of life-history traits from 48 to 26. Ordinal data were treated as numerical semiquantitative data, as the differences between functional states were approximately equal. Wingspan and commonness were log-transformed (log(X + 1)) to mitigate their large range compared to other life-history traits and to address the skewness in commonness.

Table R (environmental characteristics table):

Similar to Table Q, I applied logarithmic transformation to the environmental variables to standardize the data.

I began by testing correlations between individual environmental variables (environmental variable x environmental variable) and then between individual life-history trait variables (life-history trait variable x life-history trait variable) to identify possible strong positive or negative relationships. After that I noted these strong and very strong relationships to aid me in discussing the results of the following analyses. I used the Pearson correlation coefficient with the *corrplot* function in the corrplot package (Wei and Simko, 2021) in R version 4.4.0 (R Core Team, 2024).

To explore the relationships between environmental variables (R), species traits (Q), and species composition (L) to identify how environmental gradients influence trait-based community structure, I used the RLQ analysis, developed by Legendre et al. (1997) and later refined by Dray et al. (2014). Unlike any two-table methods, RLQ analysis integrates three data matrices: table R (environmental variables x plots), table L (plots x species abundance), and table Q (species x traits), allowing relationships between moth traits and environmental variables to be assessed based on species distribution across plots.

The RLQ analysis involves several steps. First, I applied Correspondence Analysis (CA) to table L, which assigned scores to species and plots by maximizing inertia between plots and species abundance. Since table R contains quantitative data, I used Principal Component Analysis (PCA) for this table, while using the column weights from the CA. For table Q, which includes both quantitative and categorical variables, I used Hill-Smith analysis to accommodate the mixed data types, while using the row weights from the CA. Finally, I computed the RLQ analysis. Results are provided graphically using the main axes of co-variation between functional moth traits and environmental characteristics. RLQ analysis was conducted in R version 4.4.0 (R Core Team, 2024) using the *ade4* package (Dray & Siberchicot, 2017)

To identify moth functional groups, I used the species scores, which I gained from the RLQ analysis. To find the optimal number of clusters I used the Average Silhouette Method and Calinski–Harabasz Method. The Average Silhouette Method assesses the quality of clustering by measuring how well each data point fits within its assigned cluster compared to other clusters (Rousseeuw, 1987; Halkidi et al. 2001). For each point, a silhouette score is calculated as the difference between the average distance to all points within the same cluster (a – cluster tightness) and the average distance to points in the nearest neighboring cluster (b – cluster separation), divided by the maximum of a and b, which results in the Silhouette coefficient. This score ranges from -1 to +1, where values close to +1 indicate well-clustered points, values near 0 suggest points on the boundary, and negative values indicate similarity to other clusters. By calculating the average silhouette score across all points for different numbers of clusters, the optimal number of clusters can be identified as the one that maximizes the average silhouette score, indicating the most distinct separation between clusters. To calculate the Average Silhouette score, I used the function fviz_nbclust in the *factoextra* package (Kassambara & Mundt, 2017). To visualize how the species split into clusters I used Cluster dendrogram using the “ward.D2” method which helped me identify the species belonging in each cluster.

The Calinski–Harabasz (CH) method (also known as the Variance Ratio Criterion) differs from the Average Silhouette Method in that it measures clustering quality by assessing the ratio of *between-cluster variance* to *within-cluster variance* (Calinski & Harabasz, 1974). Specifically, the CH score is calculated by dividing the sum of squared distances between cluster centers (BCSS, indicating separation) by the sum of squared distances of observations within clusters to their respective cluster centers (WCSS, indicating compactness), then scaling by the number of clusters and observations. A higher CH score indicates better-defined clusters (CH score can go up to infinity), favoring clusters that are well-separated and internally compact. Unlike the Average Silhouette Method, which focuses on individual points' cohesion and separation, the CH method evaluates overall cluster separation and cohesion at a more aggregate level, making it computationally efficient but less sensitive to nuanced boundary placements. To calculate the Calinski–Harabasz score, I used the function calinhara in *fpc* package (Hennig & Imports, 2015). To visualize life-history traits of clustered groups, I used violin plots with the *ggplot2* package (Wickham et al., 2016) and added random variation to the points using the geom_jitter function, facilitating clearer visualization in R version 4.4.0 (R Core Team, 2024). Based on visual analysis of the violin plots I chose several life-history traits, which seemed to significantly differ. To determine the appropriate statistical method, I first tested the normality of life-history trait data for each group using the Shapiro-Wilk test. If the data significantly deviated from normality ($p < 0.05$), I applied the Kruskal-Wallis test to find out if the groups significantly differed; otherwise ($p > 0.05$), I used a one-way ANOVA.

I also conducted a Fourth-corner analysis, developed by Dolédec et al. (1996) to assess the relationships between species traits (Q) and environmental variables (R) by testing pairwise associations. The Fourth-corner analysis evaluates these relationships one trait and one environmental variable at a time while accounting for species distribution across samples. To test these pairwise associations, specific permutation models are applied. In Model 2, the rows of the R table (samples) are permuted, testing the null hypothesis that species distributions with fixed traits are not influenced by environmental conditions. In contrast, Model 4 permutes the rows of the Q table (species), testing whether species traits influence assemblage composition given fixed environmental conditions. By combining these two models (Model 6), the null hypothesis of no relationship between traits and environmental variables is robustly evaluated.

For each pairwise association, two p-values (from Models 2 and 4) are combined, typically taking the maximum p-value to ensure a conservative test. Multiple testing correction (e.g., False Discovery Rate, FDR) is applied to control for inflated error rates. To increase statistical power, I set the number of permutations to 49,999. This high number enhances the detection of significant relationships, especially when working with a high number of variables (Dray et al. 2014). To adjust for multiple testing, I applied the false discovery rate method (FDR) by Benjamini and Hochberg (1995). I conducted the analysis in R version 4.4.0 (R Core Team, 2024) using the *ade4* package (Dray & Siberchicot, 2017).

Finally, I applied the Combined RLQ-Fourth Corner method, as introduced by Dray et al. (2014), to identify significant relationships between individual life-history traits, environmental variables, and the RLQ ordination axes. In other words, which life-history traits and which environmental variables were significantly associated with the disturbance gradient. This test uses the results of RLQ analysis and the Fourth-corner analysis and then works with them further. I conducted a global test, which is a multivariate statistic, based on the sum of RLQ eigenvalues, which assesses the overall relationship between traits and environment, with a null hypothesis that there is no significant relationship between life-history traits, environmental variables and RLQ ordination axes.

Subsequently, I conducted significance testing of the RLQ outputs. Fourth-corner tests are applied directly to the RLQ ordination scores (traits and environmental gradients). This reduces dimensionality and focuses on the most important axes of variation identified in RLQ. This approach is particularly effective for datasets with numerous interacting variables, as in my thesis. I conducted the analysis in R version 4.4.0 (R Core Team, 2024) using the *ade4* package (Dray & Siberchicot, 2017).

To analyze the response of community-level trait composition to environmental gradients and enhance the robustness of my results, I applied Community-Weighted Mean Redundancy Analysis (CWM-RDA). This method evaluates how community-weighted mean traits (CWMs) respond to environmental variables, focusing on the community level rather than species-level responses (Kleyer et al. 2012). In the first step, I calculated CWMs, creating a plot-by-trait matrix by weighing species trait values by their relative abundances within each plot. For continuous traits, CWMs were computed as weighted means, while for categorical traits, they were represented as weighted proportions of species possessing a given trait. To ensure compatibility, all categorical traits were converted to binary form (dummy variables). In the second step, I performed partial Redundancy Analysis (RDA), conditioning on the pseudoreplication groups as covariates to account for variation explained by the group structure. This step tested the extent to which environmental gradients explained the variation in community-weighted traits. To identify the most significant environmental variables, I applied forward selection to the CWM-RDA results using the *ordiR2step* function from the *vegan* package (Oksanen et al., 2013) in R version 4.4.0 (R Core Team, 2024). Forward selection sequentially adds the environmental variables that explain the largest portion of the remaining variation in community-weighted means (CWMs), while accounting for the pseudoreplication group effect. Statistical significance at each step was assessed using permutation tests with 999 permutations.

Results

Moth diversity patterns

The GEE analyses revealed a significant effect of disturbance intensity on moth species diversity. Following post-hoc tests showed that plots with very low disturbance intensity (IV) hosted the highest species diversity compared to the other plots. The highest species richness was recorded in least disturbed plots (IV) (Tab. 1). Following analysis, species richness showed significant difference between the plots with very low disturbance intensity and all the other disturbance diversities, while Chao1 index only showed a significant difference in estimated species richness between the plots with very low disturbance intensity and the plots with high disturbance intensity (Fig. 3). Meanwhile Shannon diversity index and Simpson diversity index showed a significant difference only between plots with low and medium disturbance intensity, but Shannon diversity index also showed a significant difference between medium and very low disturbance intensity (Fig. 3).

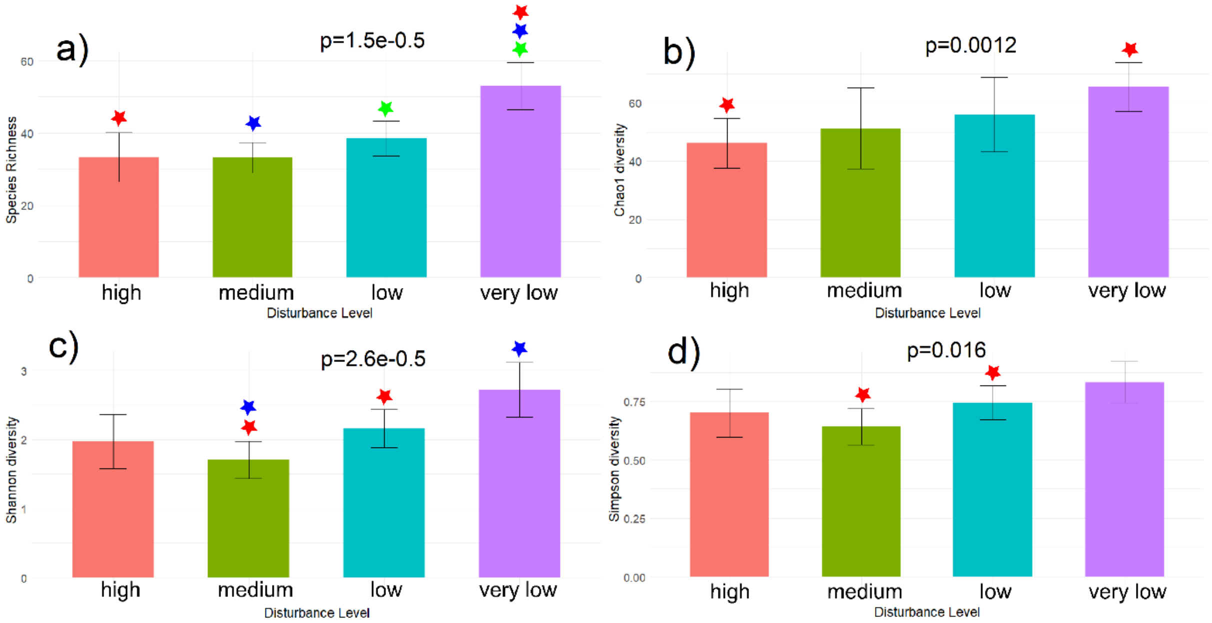


Fig. 3 – Results of the GEE analyses of moth species richness and diversity indices among different disturbance intensity levels in artillery shooting areas in the Brdy Mts. Bars represent estimated marginal means, while error bars represent 95% confidence intervals. P-values are derived from the Wald statistic of ANOVA on the GEE models. Stars with the same color represent a significant difference between the two disturbance levels. a) species richness, b) Chao1 index, c) Shannon diversity index, d) Simpson diversity index

Plots	Species richness	Shannon diversity index	Simpson diversity index	Chao1 diversity index
Jordán I-1	28	2.773	0.883	55.200
Jordán I-2	46	2.699	0.839	71.667
Jordán I-3	27	1.597	0.618	40.000
Jordán II-1	48	1.780	0.636	90.857
Jordán II-2	39	2.429	0.833	96.750
Jordán II-3	28	1.562	0.616	33.143
Jordán III-1	50	2.264	0.773	104.167
Jordán III-2	55	2.813	0.873	100.111
Jordán III-3	44	1.754	0.611	61.273
Jordán IV-1	64	2.670	0.810	91.000
Jordán IV-2	63	2.009	0.660	113.750
Jordán IV-3	83	2.505	0.768	110.000
Tok I-1	35	1.758	0.692	62.143
Tok I-2	38	1.508	0.516	55.500
Tok I-3	51	1.920	0.703	66.545
Tok II-1	38	1.440	0.568	61.750
Tok II-2	33	1.515	0.565	46.000
Tok II-3	28	1.665	0.660	39.000
Tok III-1	36	2.447	0.810	46.500
Tok III-2	38	1.996	0.688	60.667
Tok III-3	34	2.000	0.740	54.000
Tok IV-1	44	3.032	0.919	63.125
Tok IV-2	55	3.288	0.934	76.375
Tok IV-3	66	3.311	0.934	99.067

Table 1 – Diversity of moths at individual study plots under different intensity of military disturbances in the Jordán and Tok artillery ranges. Roman numerals indicate disturbance intensity (IV = very low, III = low, II = medium, I = high), while numbers specify grouping into blocks.

Main relationships between species traits and environmental variables

Pearson's correlation analysis revealed several strong and very strong relationships among particular environmental characteristics of the study plots. Some correlations were high due to variable similarities, such as the very strong correlation between E3 vegetation level and tree cover (0.96). Others reflected ecological patterns, such as the very strong negative correlation between heath cover and tree cover (-0.81). Notably, disturbance intensity exhibited some important correlations. There were very strong negative correlations with E3 vegetation level (-0.88), tree cover (-0.84), coniferous tree cover (-0.69), and E0 vegetation cover (-0.55). In contrast, strong positive correlations were observed with heath cover (0.62) and E1 vegetation level (0.53), while the positive correlation with bare ground (0.49) was also noteworthy (Fig. 4).

Most correlations among life-history traits appear to result from the methods used to calculate the variables. For instance, the strong negative correlation between mesophilous1 (MES1) or xerophilous (XER1) and vegetation complexity preference (TDST) arises because TDST is derived from habitat-specific preferences: species classified as both MES1 and XER1 receive a vegetation complexity value of 1, whereas species categorized as MES2 and MES3 are assigned a value of 2.5 (the average of 2 and 3; see Potocký et al. 2018 or the Methods and Materials chapter). Other correlations, such as the one between lichen feeders and hairy larvae (0.75; Fig. 5), are less straightforward.

The RLQ analysis revealed the relationships between species traits (Q), environmental variables (R), and species distribution (L) and the main axes of variation.

The first axis (Axis 1) accounted for 91.84% of the total variation in the data (eigenvalue = 4.452; total inertia = 4.847). The second axis (Axis 2) contributed an additional 5.20% of the explained variability, summing the cumulative variance explained by the first two axes to 97.04%. The following axes (Axes 3–5) explained less than 1 % of the variation each and had minimal contributions to the explained variability, which means that the first two axes capture nearly all of the meaningful variability in the data. The correlation between environmental variables and life-history traits can be described using their RLQ coefficients, specifically their positions on the RLQ1 axis (x-axis). The main gradient was strongly associated with disturbance intensity (DISINT; -0.826), heath cover (HEATH; -0.799), and bare ground (BARGRD; -0.427) on one side, and positively with tree cover (TRECOV; 0.826), E3 vegetation level (E3; 0.825), and deciduous tree cover (0.573) (Fig. 7a).

The visualization of RLQ results indicated that more intensively disturbed plots were colonized by species such as *Pachycnemia hippocastanaria*, *Idaea sylvestraria*, and *Eilema lutarella* (Fig. 6a). These species favored warm habitats (HATE; -0.618), dry conditions (XER1.1; -1.391 and XER2.1; -1.063), and open habitats (MES3.0; -1.060 and MES1.1; -1.097). Their larvae were often hairy (HAIR.1; -0.724) and fed on lichens (HPF5; -0.830) or detritus (DETR1.1; -1.555) (Fig. 7b). Oppositely, plots with lower disturbance intensity were inhabited by species such as *Ochropacha duplaris*, *Tetheela fluctuosa*, and *Ptilodon capucina* (Fig. 6a). These species preferred more closed habitats (TDST; 0.827 and MES3.1; 0.573), humid conditions (HAHU; 0.587 and HYG2.1; 0.645), and had larvae that fed on trees (HPF4; 1.222). These species also frequently had an early spring flight period (0.955) (Fig. 7b).

The life-history traits least correlated with the disturbance gradient (RLQ1 axis scores < 0.100) included voltinism (VOLT; 0.021), non-early spring flying period (EASP.0; -0.043), mesophilous semi-closed habitat preference (MES2.1; -0.044), leaf consumption by larvae (LEAF.1; 0.042), flying period length (FPL; 0.070), and non-autumn flying period (AUTM.0; 0.086).

Using the Average Silhouette Method, species scores from the RLQ analysis were best represented by two clusters (Fig. 8a), visualized in Figure 9. These clusters align distinctly with disturbance intensity across the plots. Functional Group B includes species associated with disturbed, early-successional habitats characterized by low vegetation cover and extreme conditions, and is therefore termed the Disturbance-dependent group. In contrast, Functional Group A comprises species favoring stable, mid-to-late successional habitats with minimal disturbance, and is referred to as the Disturbance-sensitive group.

Several significant differences were found between the life-history traits of Disturbance-dependent and Disturbance-sensitive groups (Tab. 2). They significantly differed in their habitat preferences (habitat temperature (HATE), habitat humidity (HAHU) and vegetation complexity preference (TDST)), overwintering stage (OWST), host plant form (HPF), the occurrence of detritivory (DETR) and early spring flying period (EASP). Interestingly, they did not show a significant difference in their habitat or dietary specialization (HABR, TRRA), commonness (COMM) and not even in the other flying periods (SPRG, AUTM), flying period length (FPL) or voltinism (VOLT).

Disturbance-dependent group demonstrates a statistically significant preference for warmer, drier and more open habitats (Tab. 2, Fig. 7e, 7d and7f). Species within the Disturbance-dependent group predominantly overwinter as larvae, whereas species in Disturbance-sensitive group exhibit a more generalized overwintering strategy, primarily overwintering as either larvae or pupae (Tab. 2, Fig. 10a). The host plants of the Disturbance-dependent group are evenly distributed across all forms (forbs, grasses, shrubs, trees, and lichens) (Tab. 2, Fig. 10b). In contrast, the Disturbance-sensitive group shows a statistically significant preference for trees and shrubs, with only minimal feeding on other host plant forms (Tab. 2, Fig. 10b). The Disturbance-dependent group comprises nearly all detritivore species, with ten species exhibiting this trait, whereas Disturbance-sensitive group includes only one detritivore species (Tab. 2, Fig. 10c).

Interestingly, the Calinski–Harabasz index indicated an optimal clustering solution of seven groups, which differed heavily from the Silhouette method (Fig. 8b). When I plotted these seven clusters (Fig. 9), I observed that the original two clusters had split into four subgroups from Disturbance-sensitive group and three subgroups from Disturbance-dependent group: Disturbance-dependent group divided into groups B, D, and G, while Disturbance-sensitive group divided into groups A, C, E and F. The clusters were ordered along a disturbance intensity gradient as follows: group G, group B, group D, group F, group A, group E and group C. As I could not identify a relevant biological interpretation for the separation of these groups, I did not include them in subsequent analyses.

The results of the CWM-RDA analysis corroborated the findings from the RLQ analysis, highlighting habitat characteristics as the variables most closely associated with the main axis (Fig. 11). The environmental variables explained 86.57% of the variation in the community-weighted means of life-history traits. Specifically, the first axis of the CWM-RDA accounted for 47.13% of the variation (Eigenvalue of 0.84), while the second axis explained 16.96% (Eigenvalue of 0.15, with both axes together capturing 64.04% of the total variation.

For the RDA analysis of the patterns of moth life-history traits CWMs, the forward selection retained only disturbance intensity and heath cover ($p < 0.05$) (Fig. 12). The adjusted R^2 (a measure of the proportion of variance in the community-weighted mean traits explained by the environmental variables) was 0.4764, meaning that 47.64% of the variation in CWM traits is explained by the environmental variables, accounting for bias. The first axis had an eigenvalue of 0.7 and second axis had an eigenvalue of 0.05. These results are unusually high, suggesting that the disturbance gradient is very dominant compared to other gradients. The Monte Carlo test with 999 permutations had a p-value of 0.01 indicating that the observed variation has not been random.

The correlation with the primary axis (RDA1) can be interpreted using species scores. The life-history traits most positively correlated with RDA1 were xerophilous semi-closed habitat preference (XER2; 0.468), warm habitat preference (HATE; 0.465), xerophilous open habitat preference (XER1; 0.440), detritivory (DETR; 0.411), and mesophilous open habitat preference (MES1; 0.350). Oppositely, the traits most negatively correlated with RDA1 were vegetation complexity preference (TDST; -0.611), mesophilous closed habitat preference (MES3; -0.572), tree host plants (HPF4; -0.460), commonness (-0.401), and humid habitat preference (HAHU; -0.400). The least correlated life-history traits with RDA1 were voltinism (VOLT; -0.019), grass host plants (HPF2; 0.044), flying period length (FPL; -0.054), forb host plant (HPF1; 0.058) and mesophilous semi-closed habitat (MES2; 0.069).

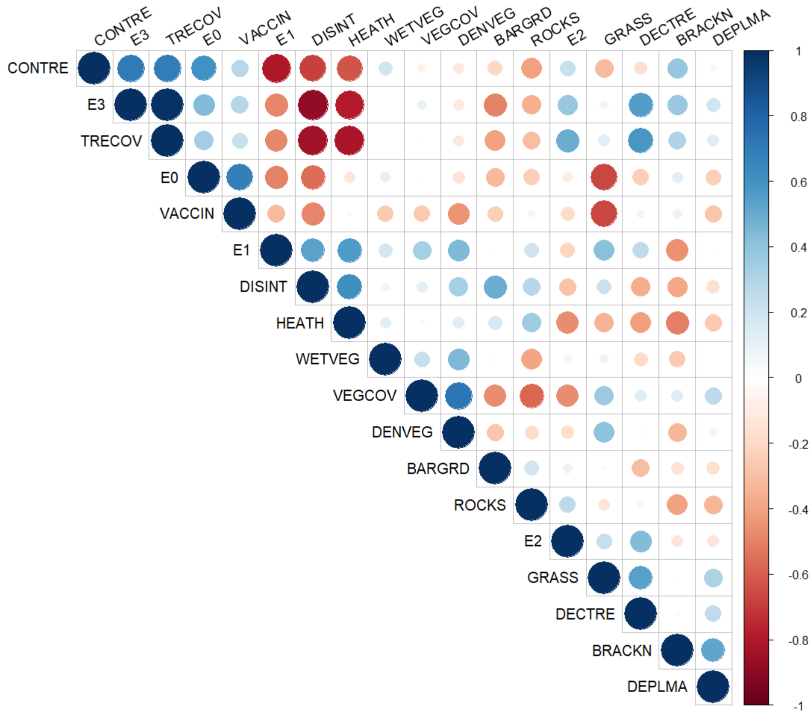


Figure 4 – The results of the Pearson's correlation coefficient on environmental variables. Blue color indicates higher positive correlation, and red color indicates higher negative correlation.

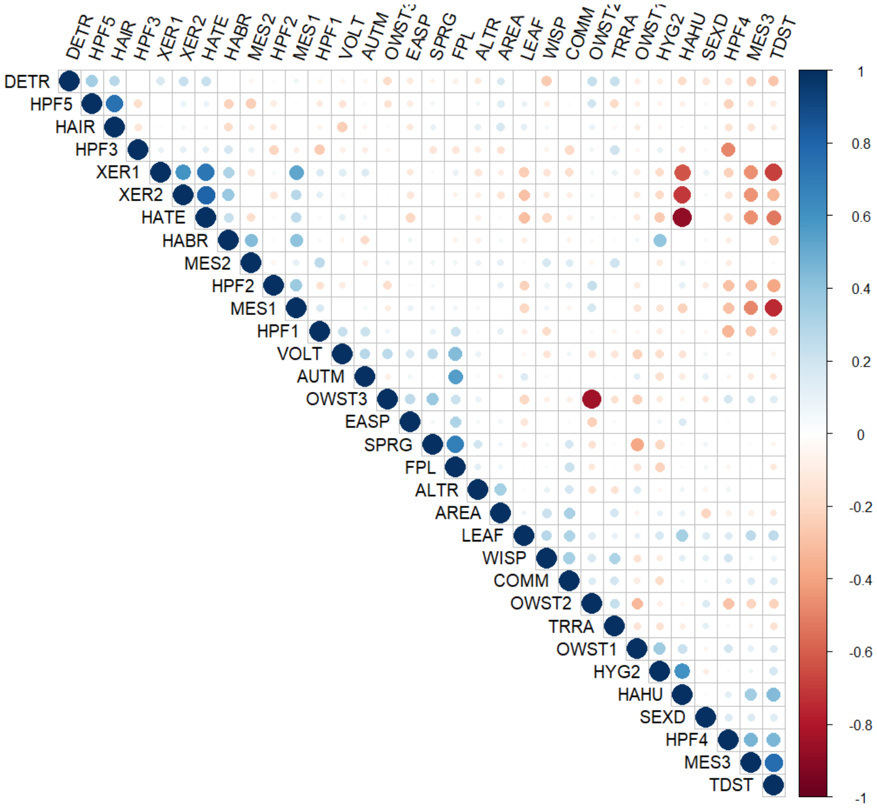


Figure 5 – The results of the Pearson's correlation coefficient on functional traits. Blue color indicates higher positive correlation, and red color indicates higher negative correlation.

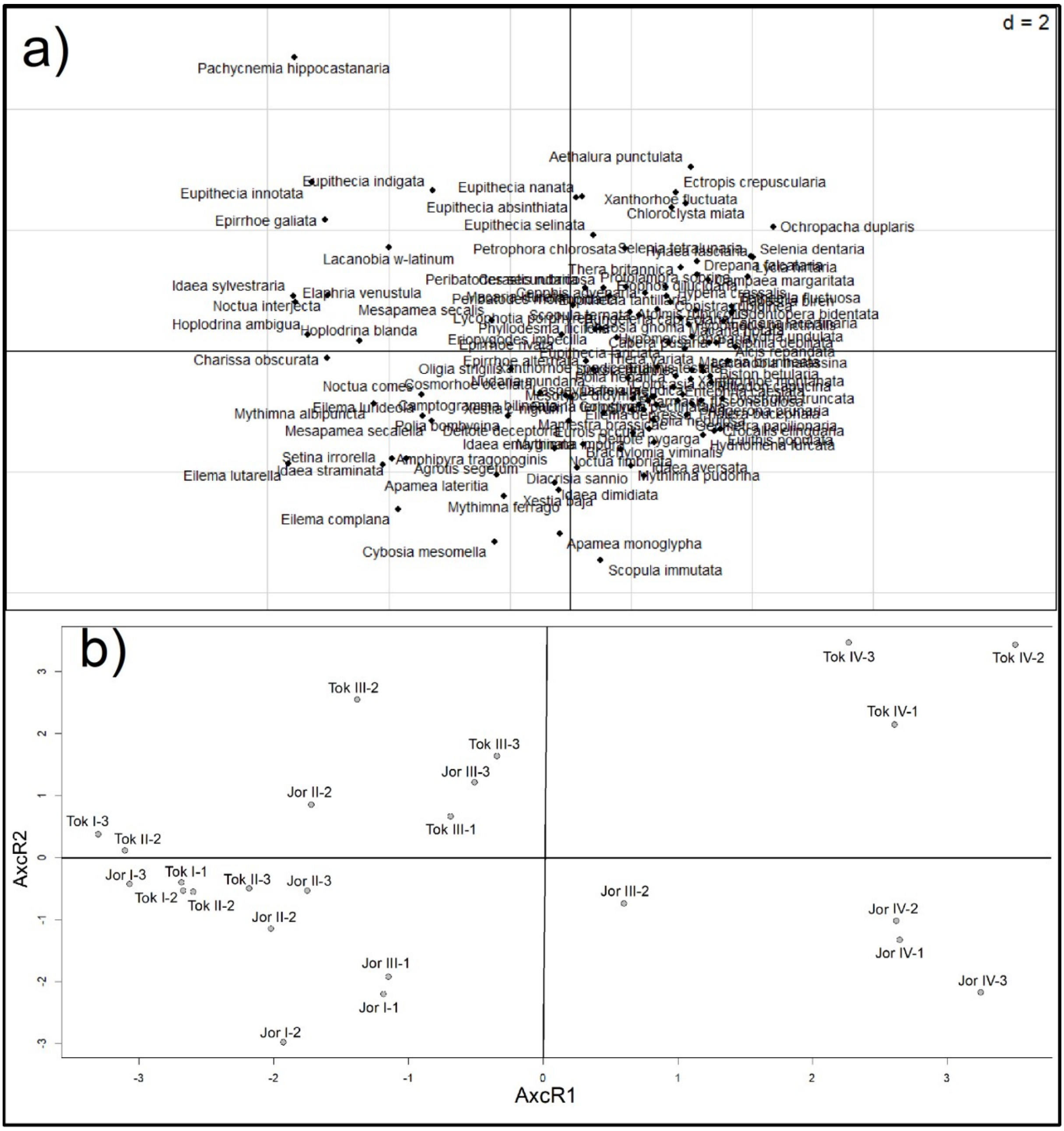


Figure 6 - Results of the first two axes of RLQ analysis representing most of the data variation. a) graph shows species scores (Q row scores), RLQ 1 axis is represented as x and RLQ 2 axis is represented as y, b) plot scores (R row scores), environmental axes AxcR1 is represented as x and AxcR2 is represented as y. Jor is an abbreviation for Jordán artillery range. Roman numerals indicate disturbance intensity (IV = very low, III = low, II = medium, I = high), while numbers specify the pseudoreplication category of individual plots (block structure). d refers to grid size.

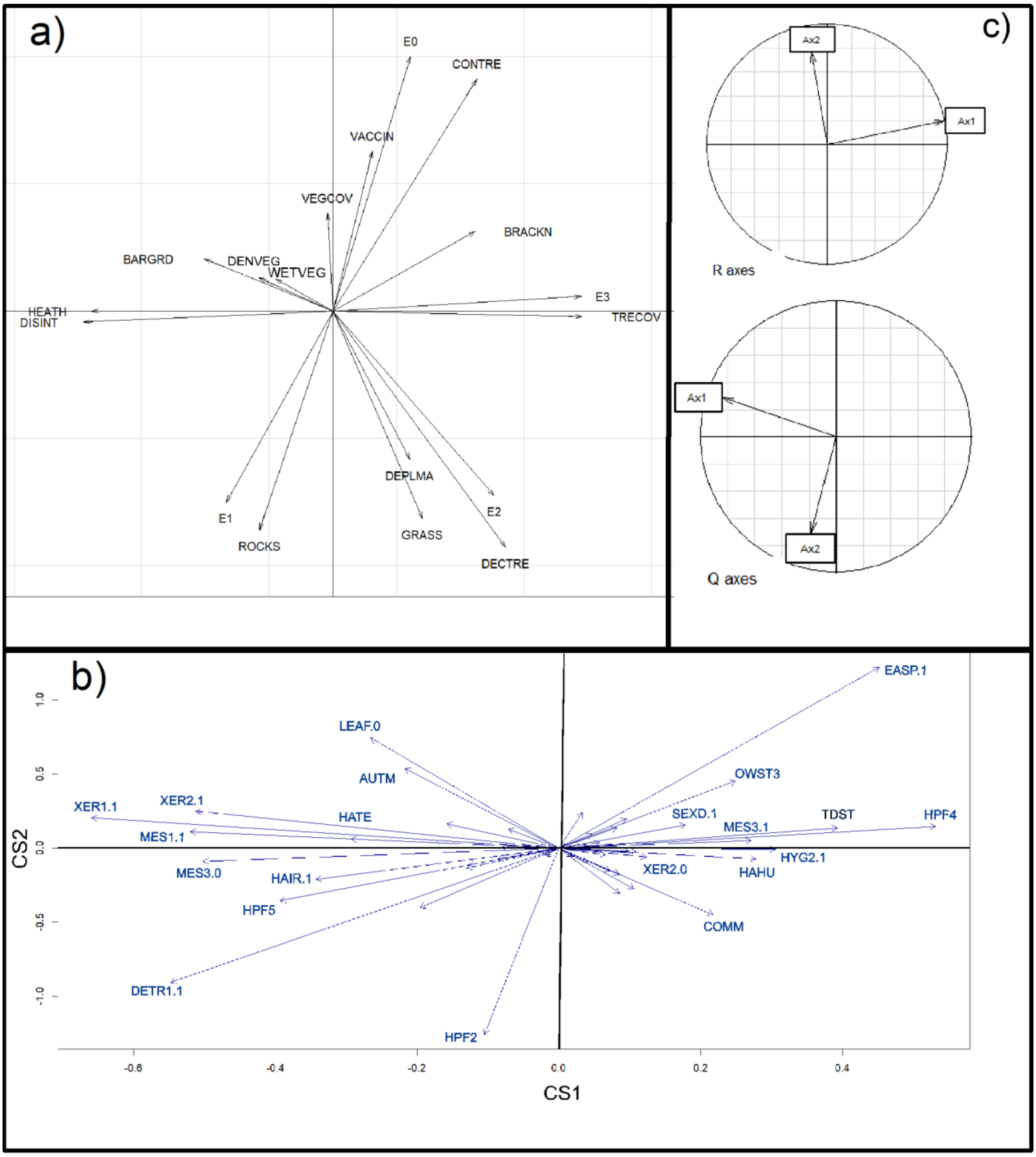


Figure 7 – Results of the first two axes of RLQ analysis representing most of the data variation. Axis 1 is represented as x and Axis 2 is represented as y. a) coefficients for environmental variables, b) coefficients for life-history traits – only ten most positively an negatively correlated with CS1 axis and top 3 with CS2 axis named, other traits were omitted to increase the clarity of the graph, c) first two axes of traits (Q axes) and environmental variables (R axes). For the abbreviations see Appendix 1.

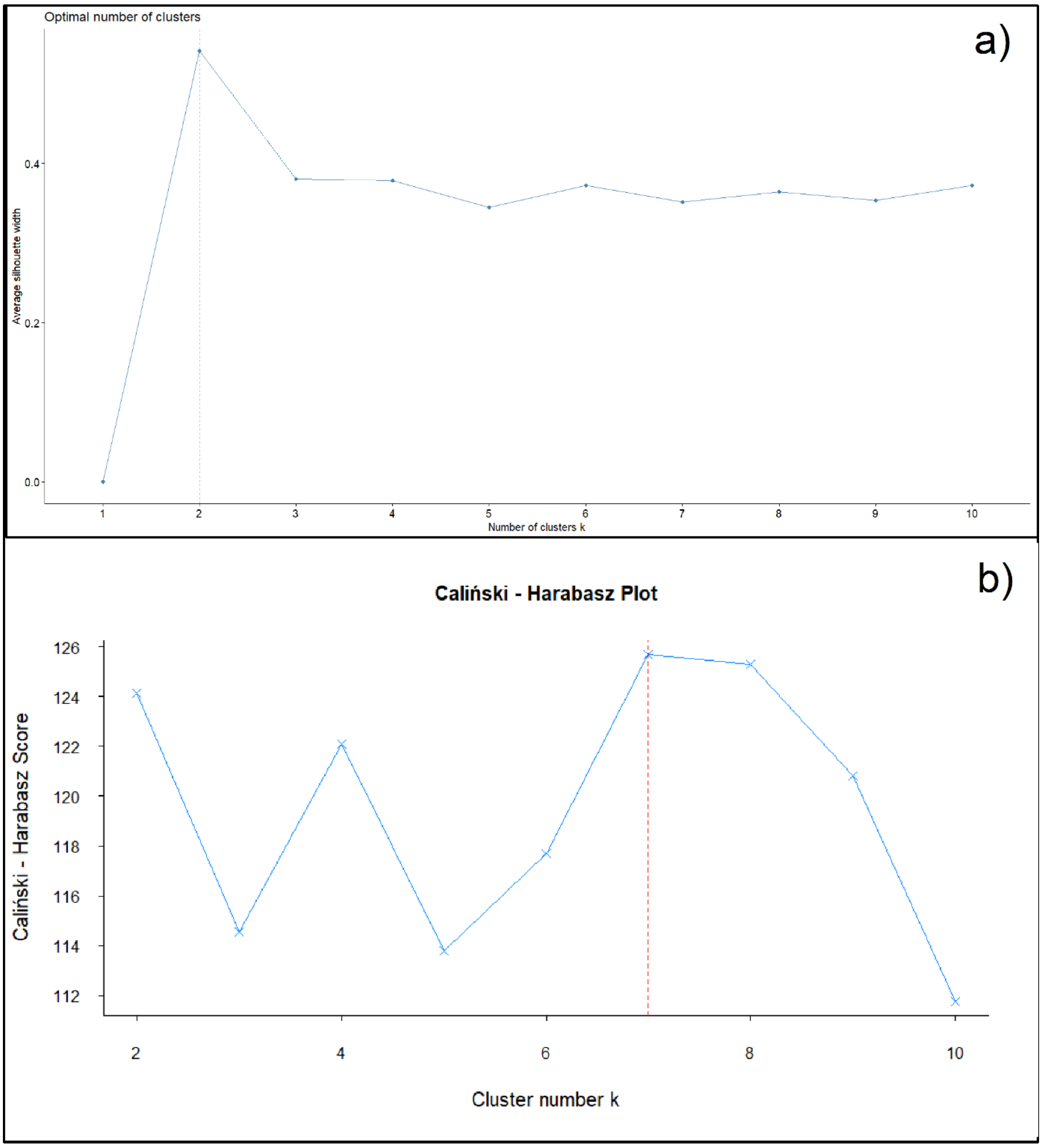


Figure 8 – The outcomes of the Average Silhouette Method (a) and the Calinski–Harabasz index (b) used to determine the optimal number of species clusters based on the species scores from RLQ analysis. Tested number of clusters was 10.

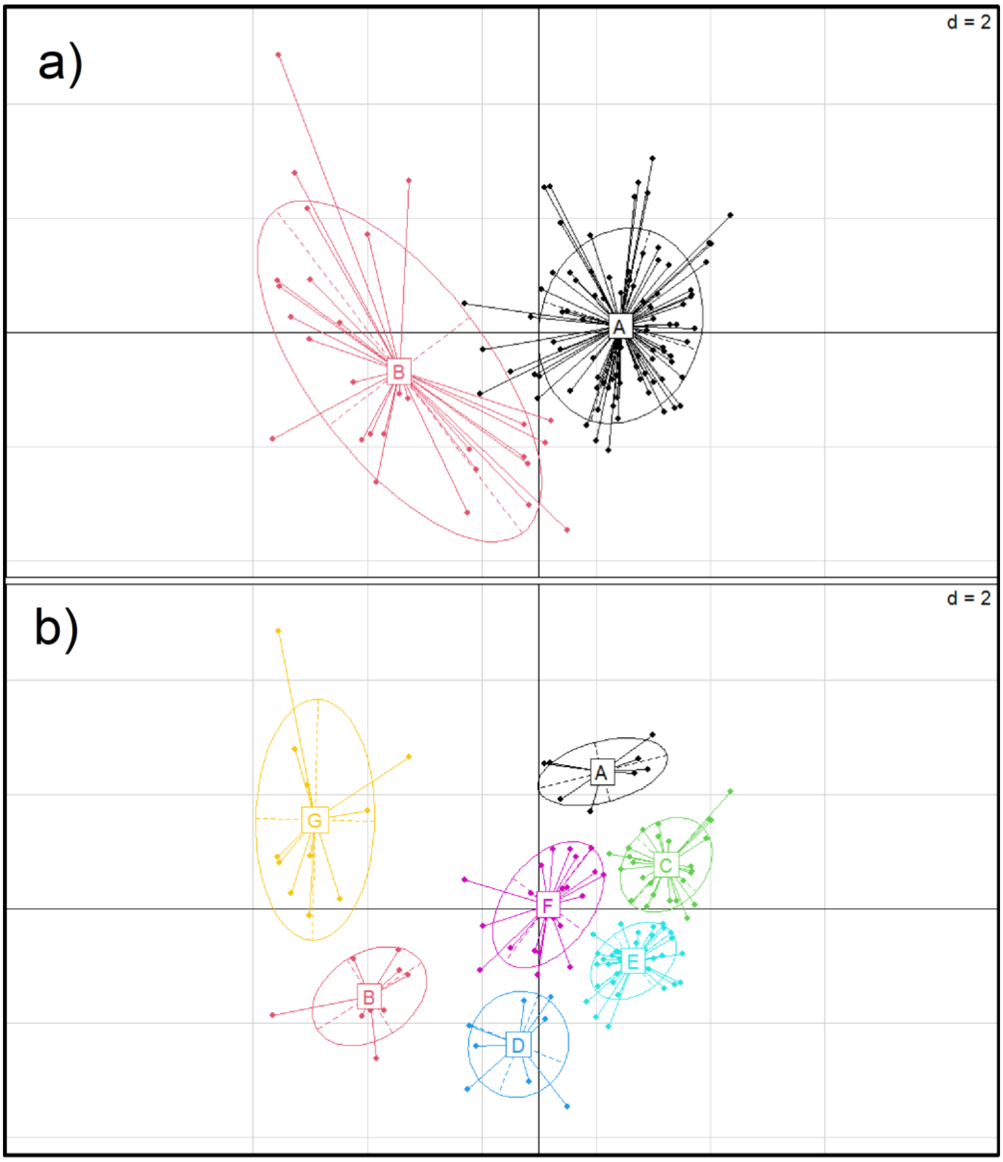


Figure 9 – The ideal clusters according to the Average Silhouette Method (A, B) and the Calinski–Harabasz index (A, B, C, D, E, F, G) tested on RLQ species scores. d refers to the grid size.

Tested functional trait	**Test type**	**Resulting p-value (<0.05)**
Vegetation complexity preference	Wilcoxon rank-sum test	9.42e-12
Habitat humidity preference	Wilcoxon rank-sum test	4.731e-10
Habitat temperature preference	Wilcoxon rank-sum test	5.804e-14
Commoness	Kruskal-Wallis test	0.303
Trophic range	Wilcoxon rank-sum test	0.166
Habitat range	Wilcoxon rank-sum test	0.233
Overwintering stage	Chi-Square test	0.017
Host plant form	Chi-Square test	0.001
Detritivory	Fisher test	2.377e-06
Autumn flying period	Fisher test	0.772

Early spring flying period	Fisher test	0.020
Larvae leaf consumption	Fisher test	0.071
Hairy larvae	Fisher test	0.071

Table 2 – Results of statistical tests comparing statistical difference between life-history traits of Disturbance-dependent group and Disturbance-sensitive group. Tested traits were determined by hypotheses and the best correlated traits with RLQ 1 axis. The choice of tests was determined by the data type (continuous, ordinal, binary, categorical with several categories). Statistically significant results (p < 0.05) are highlighted in green.

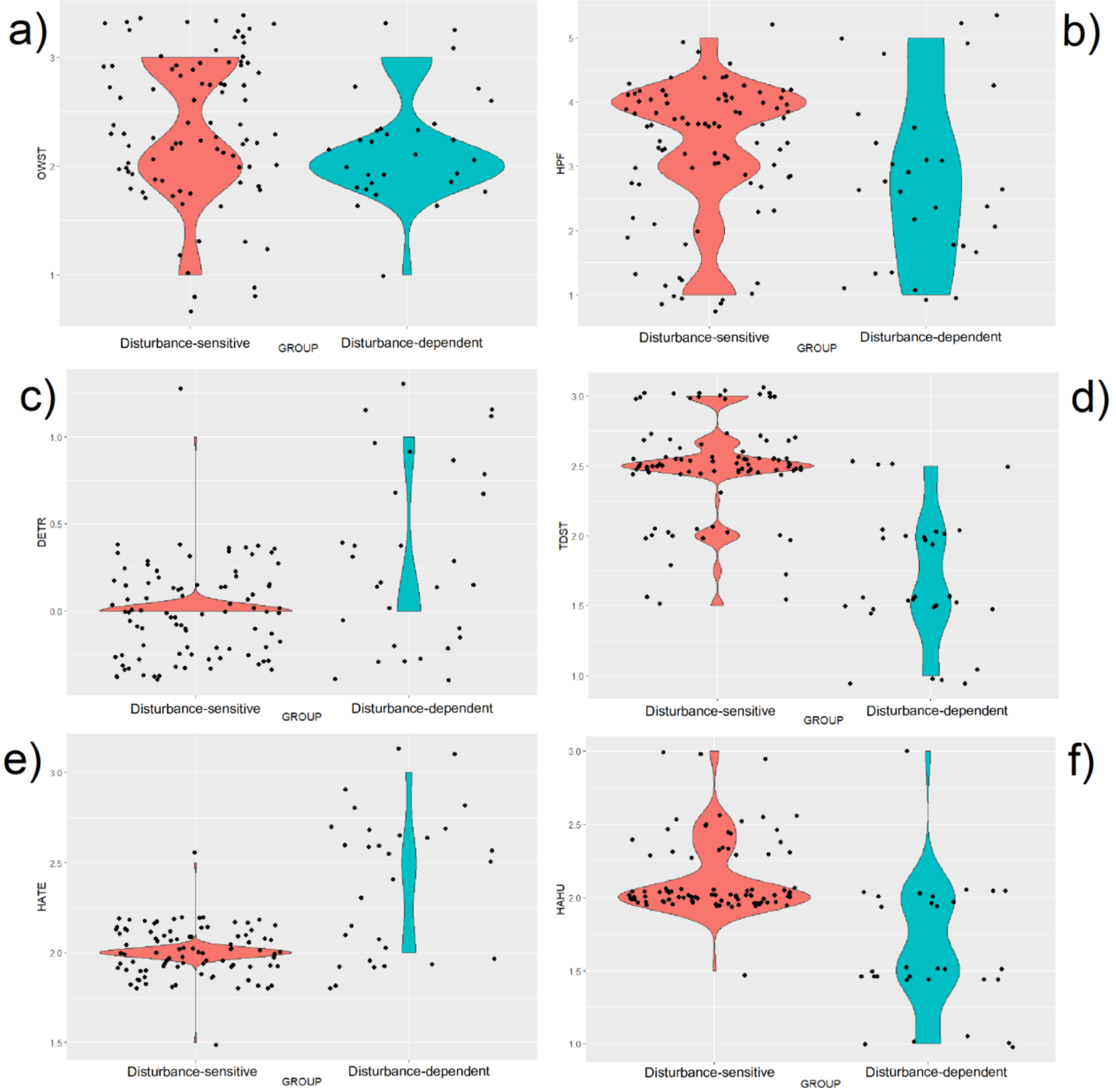


Figure 10 – Violin plots comparing the Disturbance-sensitive (red) and the Disturbance-dependent group (blue) across six variables: a) Overwintering stage (OWST – 1: egg/adult, 2: larvae, 3: pupa), b) Host plant form (HPF – 1: forbs, 2: grasses, 3: shrubs, 4: trees, 5: lichens/moss), c) Detritivory (DETR – presence or absence), d) vegetation complexity

preference (TDST – higher values indicate more complex vegetation structure, associated with succession), e) Habitat temperature (HATE – higher values represent warmer habitats), and f) Habitat humidity (HAHU – higher values represent more humid habitats). Points represent individual species, while given a slight variation with geom_jitter function.

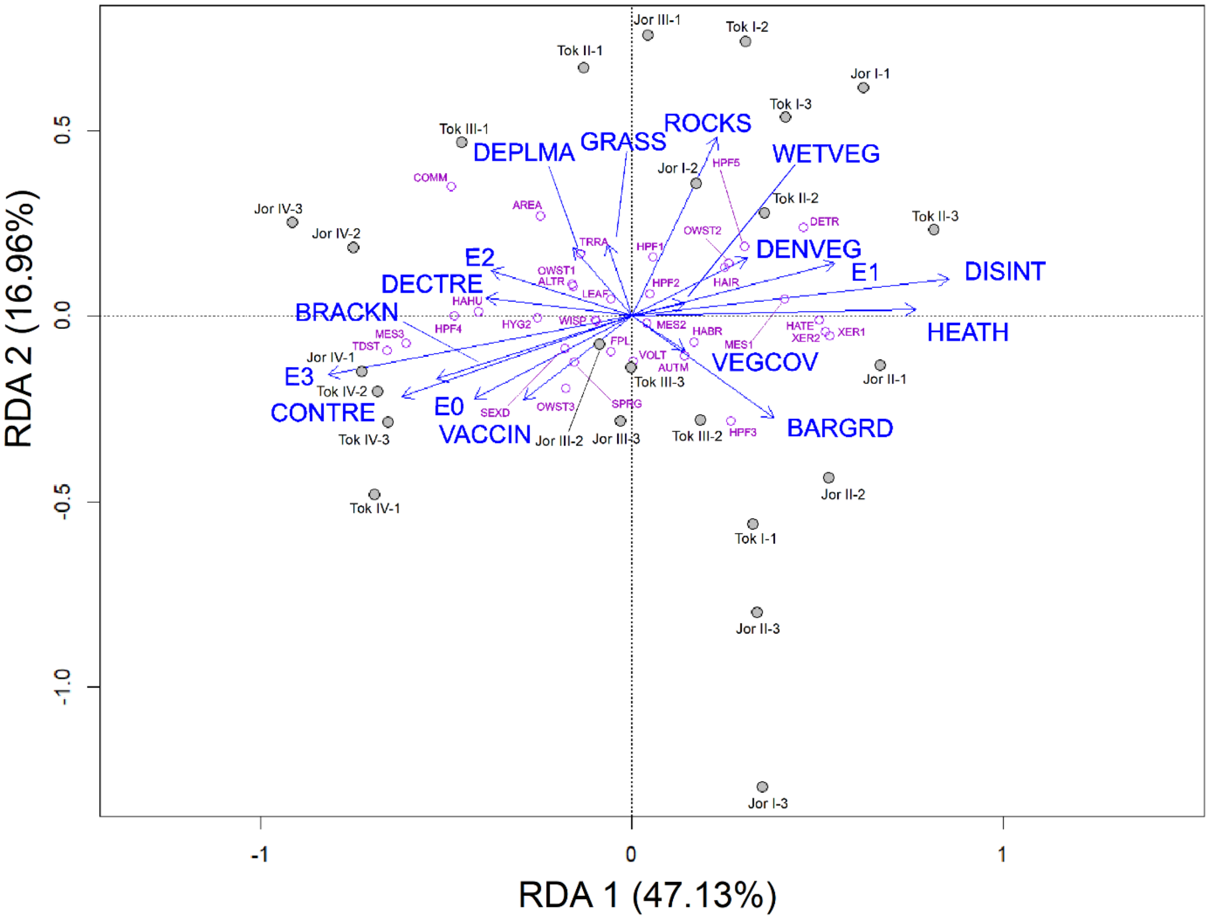


Figure 11 – The results of the CWM-RDA analysis. X axis describes 47.13% of the total variation and y axis describes 16.96%. Environmental gradients are in blue, life-history traits are in purple and plots are in black. For abbreviations see Appendix 1.

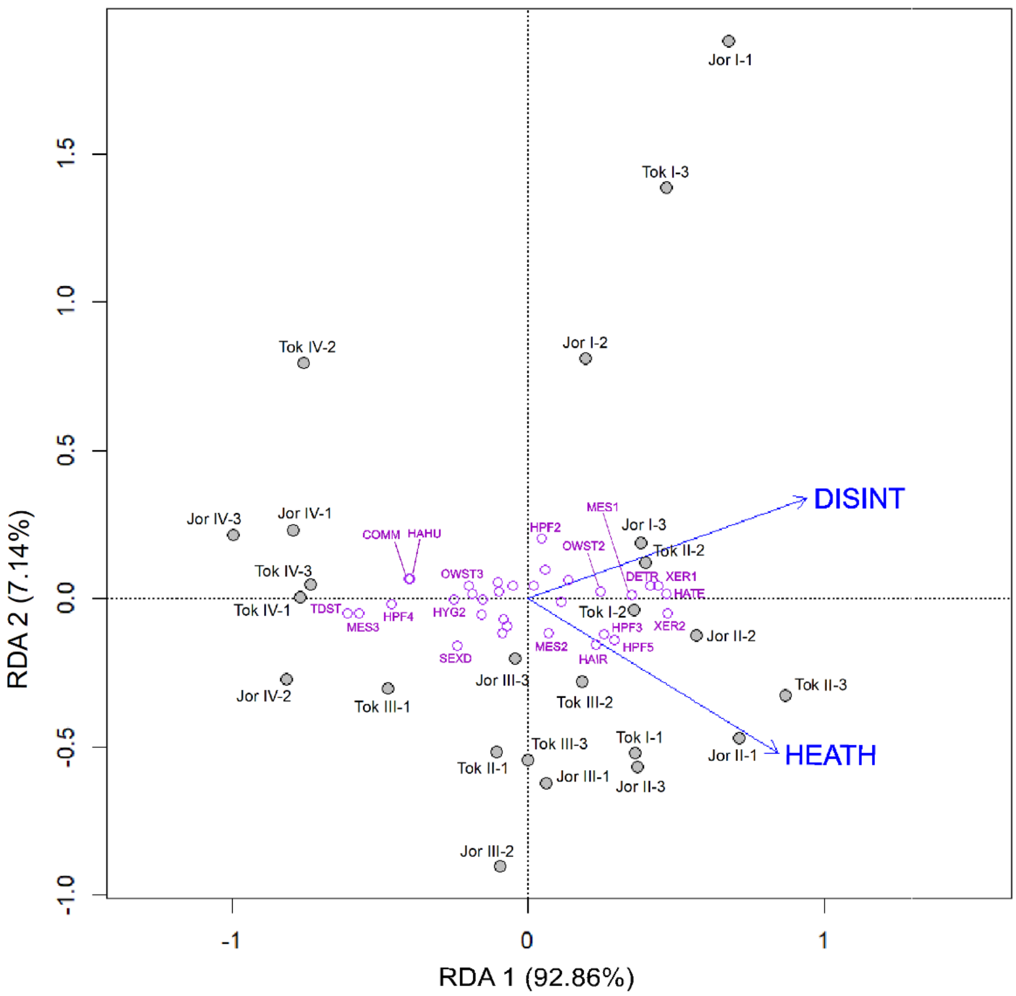


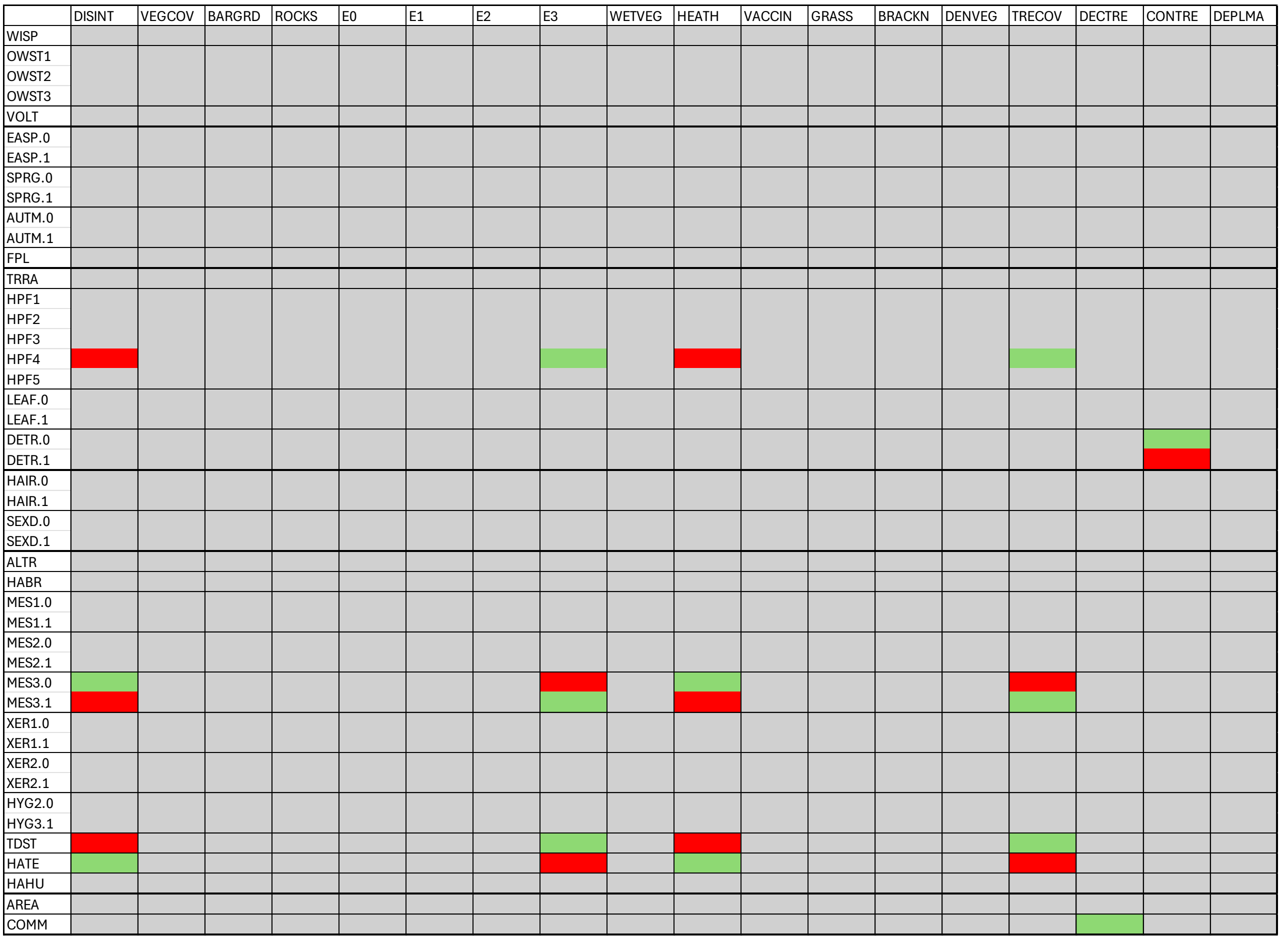
Figure 12 – The results of the CWM-RDA analysis after Forward selection. X axis describes 92.86% of the total variation and y axis describes 7.14%. Environmental gradients are in blue, life-history traits are in purple and plots are in black. Only two significant environmental variables remained with disturbance intensity (DISINT) and heath cover (HEATH). The least significant life-history traits were omitted to increase the clarity of the graph. For abbreviations see Appendix 1.

Results of Fourth corner analysis

The Fourth Corner analysis was performed to examine the bivariate associations between moth species traits and environmental variables. Every bivariate association was then tested using Monte-Carlo permutations (49 999 repetitions for robust results) on the p-value of 0.05 with FDR (false discovery rate method) applied for sequential testing.

Out of 810 possible bivariate associations, only 23 were found to be statistically significant based on the sequential approach (Fig. 13). Species with tree-feeding larvae (HPF4), mesophilous species from closed habitats (MES3.1), and those preferring higher vegetation complexity (TDST) exhibited negative associations with disturbance intensity (DISINT) and heath cover (HEATH), while showing positive associations with E3 vegetation level (E3) and tree cover (TRECOV). Conversely, non-mesophilous species of semi-open and open habitats (MES3.0) showed opposite trends, with positive associations to disturbance intensity and heath cover, and negative associations with E3 vegetation level and tree cover.

Detritivorous species (DETR.1) demonstrated a significant negative relationship with coniferous tree cover, while non-detritivorous species (DETR.0) showed a significant positive relationship. Species preferring warmer habitats (HATE) were positively associated with disturbance intensity and heath cover, but negatively associated with E3 vegetation level and tree cover. Finally, more common species (COMM) were positively associated with deciduous tree cover (DECIDS).



	DISINT	VEGCOV	BARGRD	ROCKS	E0	E1	E2	E3	WETVEG	HEATH	VACCIN	GRASS	BRACKN	DENVEG	TRECOV	DECTRE	CONTRE	DEPLMA
WISP																		
OWST1																		
OWST2																		
OWST3																		
VOLT																		
EASP.0																		
EASP.1																		
SPRG.0																		
SPRG.1																		
AUTM.0																		
AUTM.1																		
FPL																		
TRRA																		
HPF1																		
HPF2																		
HPF3																		
HPF4	🟥							🟩		🟥					🟩			
HPF5																		
LEAF.0																		
LEAF.1																		
DETR.0																	🟩	
DETR.1																	🟥	
HAIR.0																		
HAIR.1																		
SEXD.0																		
SEXD.1																		
ALTR																		
HABR																		
MES1.0																		
MES1.1																		
MES2.0																		
MES2.1																		
MES3.0	🟩							🟥		🟩					🟥			
MES3.1	🟥							🟩		🟥					🟩			
XER1.0																		
XER1.1																		
XER2.0																		
XER2.1																		
HYG2.0																		
HYG3.1																		
TDST	🟥							🟩		🟥					🟩			
HATE	🟩							🟥		🟩					🟥			
HAHU																		
AREA																		
COMM																🟩		

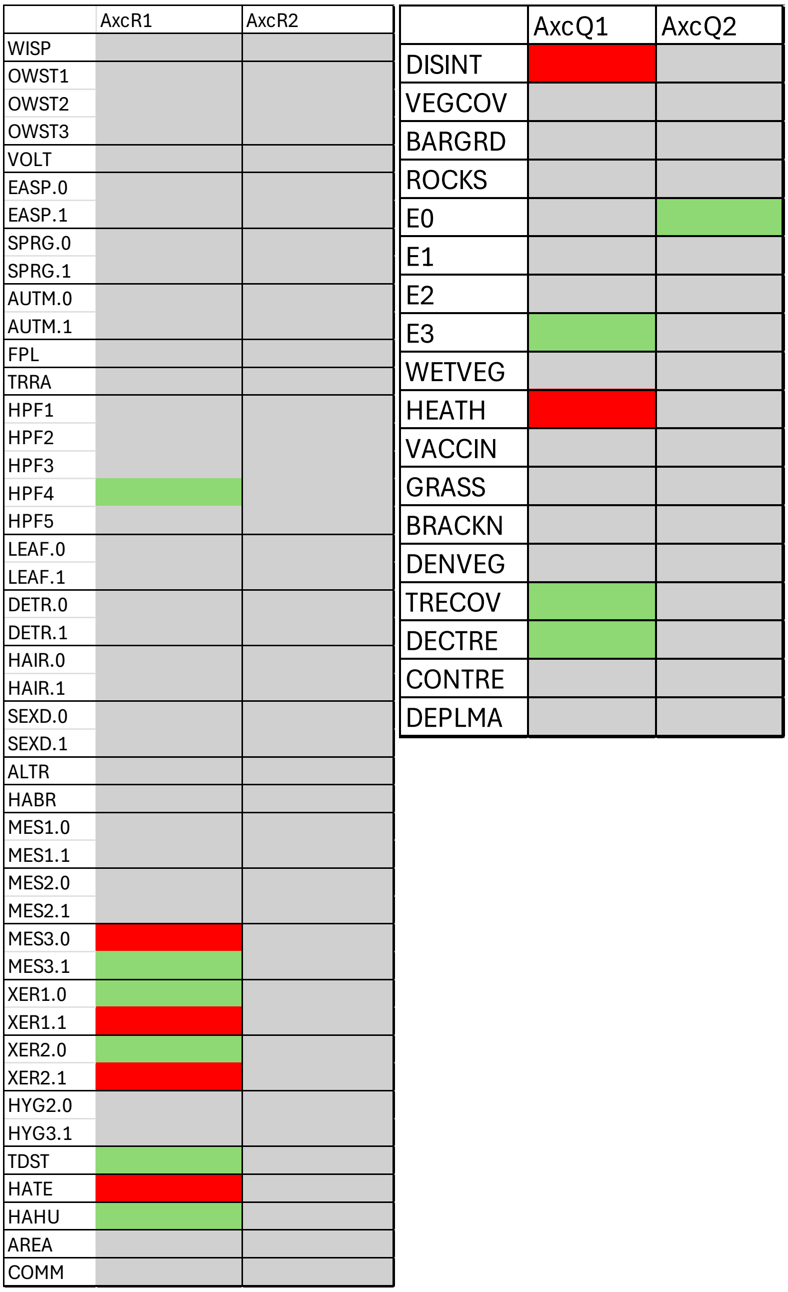
Figure 13 – The results of the Combined RLQ-Fourth corner analysis. Traits are in rows and environmental variables are in columns. Grey boxes signify no significant relationship, green boxes signify significant positive relationship, and red boxes show significant negative relationship. For abbreviations, see Appendix 1.

Results of the Combined RLQ-Fourth corner analysis

Combined RLQ-Fourth corner analysis allows me to find significant relationships between traits and environmental variables and main gradients of variation. The global permutation test for Model 6 was highly significant as the p-values of both Model 2 and Model 4 were 2e-05 (well below 0.05) allowing rejection of the null hypothesis and confirming a global relationship between functional moth traits and environmental variables.

Using the combined method, 10 of 46 possible significant associations were identified between moth functional traits and the first environmental axis (AxcR1), representing disturbance intensity, with no significant associations detected with the second environmental axis (AxcR2) (Fig. 14). The first environmental axis was positively associated with species whose larvae feed on trees (HPF.4), mesophilous species (MES3.1), non-xerophilous species (XER1.0 and XER2.0), species that prefer higher vegetation complexity (TDST), and those favoring more humid habitats (HAHU). Conversely, the axis showed significant negative associations with non-mesophilous species (MES3.0), xerophilous species (XER1.1 and XER2.1), and species that prefer warmer habitats (HATE).

The combined method also identified 6 of 26 significant associations between environmental characteristics and the first functional trait axis (AxcQ1), and one significant association with the second functional trait axis (AxcQ2) (Fig. 9). The first functional trait axis was positively related to E3 vegetation level (E3), deciduous tree cover (DECTRE) and tree cover (TRECOV) but negatively related to disturbance intensity (DISINT) and heath cover (HEATH). The second functional trait axis showed a significant positive association with E0 vegetation level (moss).



	AxcR1	AxcR2
WISP		
OWST1		
OWST2		
OWST3		
VOLT		
EASP.0		
EASP.1		
SPRG.0		
SPRG.1		
AUTM.0		
AUTM.1		
FPL		
TRRA		
HPF1		
HPF2		
HPF3		
HPF4	🟩	
HPF5		
LEAF.0		
LEAF.1		
DETR.0		
DETR.1		
HAIR.0		
HAIR.1		
SEXD.0		
SEXD.1		
ALTR		
HABR		
MES1.0		
MES1.1		
MES2.0		
MES2.1		
MES3.0	🟥	
MES3.1	🟩	
XER1.0	🟩	
XER1.1	🟥	
XER2.0	🟩	
XER2.1	🟥	
HYG2.0		
HYG3.1		
TDST	🟩	
HATE	🟥	
HAHU	🟩	
AREA		
COMM		

	AxcQ1	AxcQ2
DISINT	🟥	
VEGCOV		
BARGRD		
ROCKS		
E0		🟩
E1		
E2		
E3	🟩	
WETVEG		
HEATH	🟥	
VACCIN		
GRASS		
BRACKN		
DENVEG		
TRECOV	🟩	
DECTRE	🟩	
CONTRE		
DEPLMA		

Figure 14 - The results of the Combined RLQ-Fourth corner analysis. Grey boxes show no significant relationship, green boxes show significant positive relationship, and red boxes show significant negative relationship. On the left side is the relationship between traits and main environmental gradients (AxcR1 is the disturbance gradient) and on the right side is the relationship between environmental variables and main life-history trait gradients. For abbreviations, see Appendix 1.

Discussion

Significant life-history trends and associations on the disturbance gradient

In my study, I have evidenced the key effects of military disturbances on moth diversity and life-history traits. Species diversity varied along the disturbance gradient, with the highest values in the least disturbed areas. Such results partially support my hypothesis that moth species richness and diversity increase with decreasing disturbance intensity, as the highest recorded diversity was found in the least disturbed plots. However, a clear consistent pattern of increasing diversity along the disturbance intensity gradient could not be confirmed. I speculate that this pattern was driven by trees dominating the least disturbed plots, since tree-feeding moth species comprise about a quarter of Central European moth species (Potocký et al. 2018). Consistently, their presence in the least disturbed plots significantly contributes to the food guild and likely enhances overall species richness. Additionally, the greater biomass, primarily from tree foliage, may provide sufficient resources to support a larger number of species, reducing competition and enabling higher species coexistence (Shewring et al. 2022). This may explain why species richness is higher in these plots compared to more disturbed ones. Notably, none of the studied plots contained substantial E2 vegetation (shrubs 1–5 meters tall), thereby skipping the mid-successional stage that often supports peak diversity (Hilt & Fiedler, 2005; Habel et al. 2019), which lead to the least disturbed areas having the largest vegetation complexity and thus offering largest number of microhabitats, which is another possible explanation for highest species diversity, which has been supported by studies, which studied moth species diversity in the tropics (Hilt et al. 2006; Axmacher et al. 2004). It is also possible that the true late successional habitat was not represented in my study as the oldest forests in the area are only around 100 years old and they could have matured even further. Another possibility is that due to the nature of the disturbances and characteristic high diversity of tree-feeders between moths, the diversity-disturbance relationship is positive with decreasing disturbance intensity, which is what my results suggest.

The composition of moth species was primarily driven by habitat characteristics—openness, temperature, and humidity—as well as the presence of host plants. Moths in highly disturbed areas were associated with drier, warmer, and open habitats, while those in least disturbed areas preferred more humid, cooler, and closed habitats, which supports my hypothesis. These preferences defined two distinct functional groups: Disturbance-dependent group and Disturbance-sensitive group. This division aligns with the idea that habitat preference represents a key gradient in life-history variability among moths (Pavlíková & Konvička, 2012; Potocký et al., 2018). Habitat characteristics directly affect microclimate creating cooler but more stable temperatures, which are conditions that some species prefer. The species' habitat preference can also be linked to the occurrence of their host plants as more intensively disturbed habitats hosted only a limited number of trees, while in the least disturbed parts, they were dominant.

Both functional groups also exhibited notable differences in dietary habits. Disturbance-sensitive species were comprised mainly of tree-feeders, attracted by the high tree cover, followed by shrub feeders, likely feeding on shrub-forming trees, rowan (*Sorbus aucuparia*) or berries (*Vaccinium spp.*) (AOPK ČR, 2024b). Other host plant forms were way less. In contrast, disturbance-dependent species exhibited a more evenly distributed diet across all five host plant forms, including lichen feeders such as the critically endangered *Setina irrorella* (Erebidae). This is likely caused by the host plant heterogeneity in disturbed habitats with all forms being present in substantial numbers. Despite the higher diversity of host plant forms among disturbance-dependent species, there was no significant difference in trophic range between the groups, which means that I have to reject my hypothesis. This result is particularly interesting, as intense disturbances are often thought to filter out dietary specialists (Kitahara et al. 2000; Kirkpatrick et al. 2018). The apparent survival of specialists in highly disturbed areas could be explained by the heterogeneity of disturbance, which creates refugia allowing the survival of specialists and their host plants, or it could be caused by limitations in the life-history traits used to capture dietary specialization, which do not consider local specialization, leaving me with inaccurate results (Hughes, 2000). Nearly all detritivore species were part of the Disturbance-dependent group and exhibited a significant negative relationship with coniferous tree cover. As detritus is often only a supplementary part of their diet (Macek et al. 2007, 2008, 2012), so the species distribution was probably largely driven by their main diet or habitat preferences. For example, the only detritivore species from the Disturbance-sensitive group, *Cybosia mesomella* (Erebidae) is known to feed on moss and lichens growing on deciduous trees and thus the species low-disturbance preference aligns with its diet. On the other hand, the Disturbance-dependent detritivores were either lichen/moss feeders preferring lichens or moss growing on rocks (*Eilema complana, Eilema lutarella, Setina irorrella*) or herb-feeders (*Elaphria venustula, Hoplodrina ambigua, Idaea aversata, Idaea dimidiate, Idaea straminata, Scopula immutata*) or wide generalists (*Idaea emargianta*) (Macek et al. 2007, 2008, 2012). Additionally, the negative correlation with coniferous trees could be related to the low-quality detritus commonly found under coniferous trees, which is nutrient-poor and rich in secondary compounds, making it hard to digest and as such an unattractive source of food. The significant presence of lichen-feeders is also related to the presence of hairy larvae. Although a rare trait, most of the species with hairy larvae were disturbance-dependent lichen-feeders, which likely need larvae defenses due to them feeding on exposed rocks.

The Disturbance-sensitive group also included a significantly larger proportion of species overwintering as pupae. In moths Potocký et al. (2018) found overwintering in later stages as a part of an important voltinism gradient, where species overwintering in later stages also tended to have longer flight periods, had more generations and were more common in the Czech Republic. None of the other traits showed a significant relationship. Species overwintering as pupa (or adults) have the potential to disperse early in the year, which can be especially useful for migratory species or species whose larvae feed on early plants, especially trees (van Asch & Visser, 2007). It can also be linked to species with early flying period, maybe whose host plants emerge later in the season or species with multiple generations during the year. This trait has been linked to highly mobile and fecund generalists in butterflies (Börschig et al. 2013; Dapporto & Dennis, 2013; Bartonova et al. 2014), but this as well was not supported by other traits, such as trophic range or habitat range, both of which did not show any relevant significant relationship. Additionally, disturbance-dependent species showed significant correlation with overwintering as larvae and some correlation to autumn flying period, suggesting that their adults become active later in the year and stay active longer than disturbance-sensitive species, which oppositely showed significant correlation to early spring flying period and overwintering as pupa. The phenological difference between these groups could possibly be due to synchrony with their host plants. Synchrony between forest herbivore emergence from diapause and host budbreak is very important for its successful development and survival (van Asch & Visser, 2007). The new foliage of deciduous trees contains high nutrient amounts, which diminish later in the year and thus it encourages early-spring herbivory (Fuentealba et al. 2017; Seifert et al. 2023). On the other hand, heath (*Calluna vulgaris*), the dominant species in is an evergreen species and it can support substantial moth larvae assemblage even late in the year (Fielding, 1992). This is also supported by the significant number of disturbance-sensitive tree feeders on the one hand and the number of disturbance-dependent heath feeders on the other as discussed further. Surprisingly, species with a spring flying period showed no significant association with disturbance intensity or heath cover, thus resulting in the rejection of my hypothesis. This suggests that the patchy nature of military disturbances, which was strongest during spring (Sedláček et al. 2015), allows disturbance-dependent moths to survive in refugia, even though they are in less mobile life stages. It is also possible that rather than relying on survival disturbances, disturbance-dependent moths could depend on rapid recolonization and benefit from the newly created habitat conditions.

Moth commonness and disturbance

Commonness was in the top ten of most negatively correlated life-history traits with disturbance intensity gradient, but life-history specific did not find any significant relationship. However, there was a significant positive relationship between deciduous tree cover and moth commonness. This results in my hypothesis of negative commonness-disturbance intensity relationship being partially supported. Deciduous trees in Jordán were present in fairly high covers throughout the disturbance gradient, but the highest cover was concentrated in the least disturbed areas. On the other hand, in Tok, they have been completely absent, likely due to the more intensive disturbance regime, leading to higher dominance of *Calluna*, which prevented the establishment of birch sprouts.

The rarest species (<20 faunistic squares) recorded at both localities were *Eupithecia nanata*, *Pachycnemia hippocastanaria*, *Phyllodesma ilicifolia*, *Setina irrorella*, *Eupithecia innotata*, *Idaea sylvestraria*, and *Protolampra sobrina*. According to Macek et al. (2007, 2008, 2012), of these, four species (*E. nanata*, *P. hippocastanaria*, *I. sylvestraria*, and *P. sobrina*) feed on *Calluna vulgaris*, with the first two being dietary specialists and the latter two being generalists that include *Calluna* in their diet. *P. ilicifolia* feeds on European blueberry or young deciduous trees, *S. irrorella* is a lichen specialist, and *E. innotata* is a shrub-feeding generalist. *P. sobrina* combines feeding on European blueberry or heath before later switching to birch (*Betula pendula*).

Two additional species, *Agrotis cinerea* and *Anarta myrtilli*, represented by only one individual each, were also among the rarest species. Notably, *A. myrtilli* is a dietary specialist on *Calluna vulgaris*, while *A. cinerea* is a generalist on short herbs like *Thymus spp.* Interestingly, of the nine rarest species, only three are red-listed: *S. irrorella* (CR), *P. ilicifolia* (CR), and *P. sobrina* (NT) (Hejda et al. 2017), which could lead to the discrepancy between my results and the results of Palivcová (2018), who studied only red-listed species and who only found an ambiguous relationship between moth conservation value and deciduous tree cover.

Many of the rarest moth species captured in the plots require heath in their diet, suggesting a preference for areas with higher heath cover. In contrast, only two of the rarest species (*P. sobrina* and *P. ilicifolia*) partially feed on deciduous trees, and none appear strongly associated with them. This is supported by the negative correlation between deciduous tree cover and both disturbance intensity and heath cover. These findings indicate that high-intensity management supports several rare species, particularly those in disturbance-dependent, which includes *P. hippocastanaria*, *S. irrorella*, *E. innotata*, and *I. sylvestraria*. Conversely, deciduous trees may support a high abundance of common species due to their association with both dietary generalists and specialists, providing a wide range of niches (Niemelä, 1983; Sobek et al. 2009; Seifert et al. 2021) and due to deciduous trees being linked to highly mobile common species capable of quick colonization from far away.

Conservation strategies of heathlands in Jordán and Tok

The heathlands of Jordán and Tok are among the largest in the Czech Republic. These secondary submontane and montane heathlands are classified as *near-threatened* habitats, facing significant risks and from succession eutrophication (Chytrý et al. 2020). While the heathlands are species-poor, they host numerous rare and endangered species, including butterflies and moths, with 25 confirmed red-listed species (AOPK ČR 2024b; Hejda et al. 2017). Notable species include xerophilous moths like *Eupithecia innotata* (Geometridae) and open-habitat montane species such as the endangered *Lasiocampa quercus* (Noctuidae). These moth communities enrich regional biodiversity, which is otherwise dominated by forest species typical of the Brdy Mts. Protected Landscape Area, where forests cover over 85% of the landscape (AOPK ČR, 2016). As these open habitats depend on disturbances for maintenance, their conservation must focus on disturbance-dependent species. Without active management, natural succession will rapidly alter these environments, causing the decline of vulnerable open-habitat specialists. On a European scale, moths from nutrient-poor habitats face a particularly high risk of extinction, further emphasizing the importance of their conservation (Lintott et al. 2014).

Prescribed burning is a key management tool for heathlands, as it promotes the growth of new *Calluna vulgaris* sprouts, reduces excessive plant matter, and provides a competitive advantage to heathland vegetation (Lovegrove 2017). This process is crucial for maintaining rare species as well as diverse vegetation structure (Velle et al. 2014). Heath-feeding moths from Jordán and Tok such as *Pachycnemia hippocastanaria*, *Eupithecia nana*, and *Anarta myrtilli*, profit by gaining access to young *Calluna* leaves, which have higher nutritional value. To optimize outcomes, heathlands should be burned every 10 to 25 years using patchy or striped burns, which create unburned refugia for plants and animals. Burning during excessively dry conditions should be avoided to mitigate risks (Davies et al. 2022). Grazing or mowing, particularly with sheep, can complement fire management by further suppressing encroachment. Prescribed burning should align with the historic disturbance regime, which suggests fires predominantly occurred in late spring and late summer (Sedláček et al. 2015). Some levels of encroachment could be allowed to support ecotone species, leading to higher moth species diversity as suggested by my results.

While fire is effective, its application requires careful planning and expertise. High burn frequencies or large-scale fires can threaten sedentary species or individuals in vulnerable life stages, risking local extinctions (Sedláková & Chytrý, 1999). Conversely, infrequent burns exacerbate habitat encroachment and fuel accumulation, complicating future management efforts (Lovegrove, 2017). Fire intensity is another critical factor, as high-intensity burns can damage underground plant structures and soil fauna. Even though my findings suggest that intensively disturbed plots exhibit lower species richness, I also found that they host distinct assemblages, contributing to greater regional diversity when combined with less disturbed areas.

The shallow, rocky soils at Jordán and Tok, coupled with the area's remoteness, pose challenges for conventional management methods. Heavy machinery is impractical, and replicating the effects of artillery shell impacts—historically a key disturbance factor—is particularly difficult. Among traditional approaches, grazing by sheep or potentially bison offers a feasible solution (Rosa García et al. 2013). These animals disturb the topsoil, creating patches of bare ground and exposed rocks that serve as colonization sites for lichens and mosses. This flora is crucial for disturbance-dependent lichen feeders such as the critically endangered *Setina irrorella* (Erebidae).

A less conventional method involves the use of explosives to mimic artillery impacts. This approach could create small depressions and expose the substrate, facilitating colonization by heathland flora and fauna. However, this method is costly, requires strict safety protocols, and is further complicated by the presence of unexploded ordnance in the area. Depressions created through such disturbances are particularly important for the development of peat bogs and wetland habitats. These microhabitats are essential for wetland vegetation and support specialized moth species such as the rare *Scopula immutata* (Geometridae), which relies on wetland herbs and grasses as a food source.

The conservation of heathlands in Jordán and Tok demands a combination of prescribed fire, grazing, and potentially innovative approaches to maintain disturbance regimes and prevent habitat succession. Carefully designed management strategies, aligned with ecological and historic conditions and which should adapt to new findings, are critical for preserving these near-threatened habitats and their associated species.

Conclusion

This thesis explored how moth communities react to a disturbance intensity gradient in the Brdy Mts., focusing on species diversity, functional traits, and commonness in habitats shaped by military disturbances (physical impact of artillery shells and resulting fires). The findings point out the complex relationships between disturbance intensity, habitat characteristics, and moth life-history traits, with implications for future conservation management in former military training areas.

The results demonstrated that moth species diversity was highest in plots with very low disturbance intensity, but a clear pattern of increasing species diversity did not emerge. Moth species diversity was found to be likely driven by the presence of their host plants or microclimate preferences.

Life-history trait analysis revealed two distinct groups of moths along the disturbance gradient. Species in high-intensity disturbance areas (Disturbance-dependent group) were associated with open, warmer and drier habitats and a diverse range of host plant forms, including heath and lichens. Conversely, species in low-intensity disturbance areas (Disturbance-sensitive group) thrived in cooler, more humid environments dominated by trees. Disturbance-sensitive species also start their adult activity early in the season as opposed to disturbance-dependent species who are more active later in the year.

Negative relationship between species commonness and disturbance intensity was observed. This was supported by significant positive association between moth commonness and deciduous tree cover, indicating that common species benefit more from these habitats, while rare species do not. Rare species prefer more disturbed areas with large part of the species being linked to heath (*Calluna vulgaris*) as a food source.

To support the biodiversity of moth communities in the Brdy Mts., management strategies should incorporate a mix of prescribed burning, grazing, and potentially innovative methods to imitate artillery shell impacts. These measures should strive to maintain habitat heterogeneity, support heathland ecosystems, and accommodate the needs of both common and rare species, while maintaining high species diversity linked to the disturbance intensity gradient. Without continuous management, the disturbance-dependent species are at risk of extinction due to habitat alteration and the disappearance of their host plants.

Sources:

Allen, C. E., Zwaan, B. J., & Brakefield, P. M. (2011). Evolution of sexual dimorphism in the Lepidoptera. *Annual review of entomology*, *56*(1), 445-464.

Axmacher, J. C., Scheuermann, L., Schrumpf, M., Lyaruu, H. V., Fiedler, K., & Müller-Hohenstein, K. (2006). Effects of fire on the diversity of geometrid moths on Mt. Kilimanjaro. In *Land use change and mountain biodiversity* (pp. 69-75). CRC Press.

AOPK ČR. (2016). *Plán péče o CHKO Brdy na období 2016–2025*.

AOPK ČR (2023). *Plán péče o Národní přírodní památku Tok na období 2023–2032*.

AOPK ČR (2024a). Digitální registr Ústředního seznamu ochrany přírody. [on-line databáze; Ústřední seznam ochrany přírody]. 2024-10-10; [cit. 2024-10-10]

AOPK ČR (2024b). Nálezová databáze ochrany přírody. [on-line databáze; portal23.nature.cz]. 2024-05-15; [cit. 2024-05-15]

AOPK ČR. (2024c.). *Podnebí – Brdy - AOPK ČR*. Brdy. https://brdy.nature.cz/podnebi

Bae, Y. S., Chae, D. Y., Ju, Y. D., Bae, J. H., Kim, J. M., Ahn, N. H., & Lee, C. M. (2011). Changes of species diversity on moth communities at forest fire region in Samcheok, Korea. *Korean journal of applied entomology*, *50*(1), 7-14.

Balatka, B., & Kalvoda, J. (2006). *Geomorfologické členění reliéfu Čech*. Kartografie Praha, as.

Bartonova, A., Benes, J., & Konvicka, M. (2014). Generalist-specialist continuum and life history traits of Central European butterflies (Lepidoptera)-are we missing a part of the picture?. *European Journal of Entomology*, *111*(4), 543.

Banza, P., Macgregor, C. J., Belo, A. D., Fox, R., Pocock, M. J., & Evans, D. M. (2019). Wildfire alters the structure and seasonal dynamics of nocturnal pollen-transport networks. *Functional Ecology*, *33*(10), 1882-1892.

Benedikt, M. (2014). Osídlení a historie vojenského újezdu Brdy.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society B 57:289–300.

Börschig, C., Klein, A. M., von Wehrden, H., & Krauss, J. (2013). Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. *Basic and Applied Ecology*, *14*(7), 547-554.

Brantley, E. M., Jones, A. G., Hodson, A. M., Brown, J. W., Pogue, M. G., Suazo, M. M., & Parmenter, R. R. (2023). Short-term effects of a high-severity summer wildfire on conifer forest moth (Lepidoptera) communities in New Mexico, USA. *Environmental Entomology*, *52*(4), 606-617.

Broomandi, P., Guney, M., Kim, J. R., & Karaca, F. (2020). Soil contamination in areas impacted by military activities: a critical review. *Sustainability*, *12*(21), 9002.

Bušek, O., & Reif, J. (2017). The potential of military training areas for bird conservation in a central European landscape. *Acta Oecologica*, *84*, 34-40.

Cadotte, M. W., Mai, D. V., Jantz, S., Collins, M. D., Keele, M., & Drake, J. A. (2006). On testing the competition-colonization trade-off in a multispecies assemblage. *The American Naturalist*, *168*(5), 704-709.

Caliński, T., & Harabasz, J. (1974). A dendrite method for cluster analysis. *Communications in Statistics-theory and Methods*, *3*(1), 1-27.

Caudal, P., & Gallet, S. (2023). Khaki conservation: a review of the effects on biodiversity of worldwide military training areas. *Environmental Reviews*, *31*(3), 527-541.

Chaundy-Smart, R. F. C., Smith, S. M., Malcolm, J. R., & Bellocq, M. I. (2012). Comparison of moth communities following clear-cutting and wildfire disturbance in the southern boreal forest. *Forest Ecology and Management*, *270*, 273-281.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual review of Ecology and Systematics*, *31*(1), 343-366.

Choi, S. W. (2018). A high mountain moth assemblage quickly recovers after fire. *Annals of the Entomological Society of America*, *111*(6), 304-311.

Chytrý, M., Hájek, M., Kočí, M., Pešout, P., Roleček, J., Sádlo, J., ... & Chobot, K. (2020). Červený seznam biotopů České republiky: Red List of Habitats of the Czech Republic. *Příroda*, 1-172.

Cizek, O., Vrba, P., Benes, J., Hrazsky, Z., Koptik, J., Kucera, T., ... & Konvicka, M. (2013). Conservation potential of abandoned military areas matches that of established reserves: plants and butterflies in the Czech Republic. *PLoS One*, *8*(1), e53124.

Connell, J. H., (1978). Diversity in Tropical Rain Forests and Coral Reefs. Science 199, 1302.

Culmsee, H., Evers, B., Leikauf, T., & Wesche, K. (2021). Semi-open landscapes of former military training areas are key habitats for threatened birds. *Tuexenia*, *41*.

Dalling, J. W. (2008). Pioneer species. In *Encyclopedia of Ecology, Five-Volume Set* (pp. 2779-2782). Elsevier.

Dapporto, L., & Dennis, R. L. (2013). The generalist–specialist continuum: testing predictions for distribution and trends in British butterflies. *Biological Conservation*, *157*, 229-236.

Davies, G. M., Vandvik, V., Marrs, R., & Velle, L. G. (2022). Fire management in heather-dominated heaths and moorlands of North-West Europe. *Global Application of Prescribed Fire*, 194.

Demarais, S., Tazik, D. J., Guertin, P. J., & Jorgensen, E. E. (1999). Disturbance associated with military exercises. *Ecosystems of the World*, 385-396.

Drag, L., Hauck, D., Pokluda, P., Zimmermann, K., & Cizek, L. (2011). Demography and dispersal ability of a threatened saproxylic beetle: a mark-recapture study of the Rosalia Longicorn (Rosalia alpina). *Plos one*, *6*(6), e21345.

Dumroese, K., & Luna, T. (2016). Growing and marketing woody species to support pollinators: An emerging opportunity for forest, conservation, and native plant nurseries in the Northeastern United States. *Tree Planters' Notes. 59 (2): 49-60.*, *59*(2), 49-60.

Dvořáková, L., Hanzelka, J., Romportl, D., & Reif, J. (2024). Habitat changes explain shifts in bird community composition in abandoned military training areas: Lessons for conservation. *Journal for Nature Conservation*, *79*, 126612.

Doledec, S., D. Chessel, C. J. F. ter Braak, and S. Champely. 1996. Matching species traits to environmental variables: a new three-table ordination method. Environmental and Ecological Statistics 3:143–166.

Dray, S., & Siberchicot, M. A. (2017). Package 'ade4'. *Université de Lyon: Lyon, France*.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & ter Braak, C. J. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, *95*(1), 14-21.

Edwards, P. J. (1984). The use of fire as a management tool. In *Ecological effects of fire in South African ecosystems* (pp. 349-362). Berlin, Heidelberg: Springer Berlin Heidelberg.

Ellwanger, G., & Reiter, K. (2019). Nature conservation on decommissioned military training areas–German approaches and experiences. *Journal for nature conservation*, *49*, 1-8.

European Commission, Joint Research Centre (JRC) (2018): Fire Database in the European Forest Fire Information System (version 2-3-1). European Commission, Joint Research Centre (JRC) [Dataset] PID: http://data.europa.eu/89h/678deb39-e35f-4236-a984-42d69bf95dec

Everaerts, C., Cusson, M., & McNeil, J. N. (2000). The influence of smoke volatiles on sexual maturation and juvenile hormone biosynthesis in the black army cutworm, Actebia fennica (Lepidoptera: Noctuidae). *Insect Biochemistry and Molecular Biology*, *30*(8-9), 855-862.

Ferster, B., Leppo, B. R., Swartz, M. T., Vulinec, K., Habegger, F., & Mehring, A. (2008). Lepidoptera of Fort Indiantown Gap National Guard Training Center, Annville, Pennsylvania. *Northeastern Naturalist*, *15*(1), 141-148.

Fielding, C. (1992). *Aspects of the ecology of the Lepidoptera associated with heather Calluna vulgaris* (Doctoral dissertation, Durham University).

Fuentealba, A., Pureswaran, D., Bauce, É., & Despland, E. (2017). How does synchrony with host plant affect the performance of an outbreaking insect defoliator?. *Oecologia*, *184*, 847-857.

Fox, J. W. (2013). The intermediate disturbance hypothesis should be abandoned. *Trends in ecology & evolution*, *28*(2), 86-92.

Francl, R. (2007). *Lesní požáry V české republice Z pohledu hasičů*. Lesnická práce – nakladatelství a vydavatelství. https://www.lesprace.cz/casopis-lesnicka-prace-archiv/rocnik-86-2007/lesnicka-prace-c-08-07/lesni-pozary-v-ceske-republice-z-pohledu-hasicu

Gołdyn, B., Konwerski, S., & Błoszyk, J. (2007). Large branchiopods (Anostraca, Notostraca, Spinicaudata, Laevicaudata) of small, astatic waterbodies in the environs of Poznań (Wielkopolska Region, Western Poland). *Oceanological and Hydrobiological Studies*, *36*(4), 21-28.

Gongalsky, K. B., & Persson, T. (2013). Recovery of soil macrofauna after wildfires in boreal forests. Soil biology and biochemistry, 57, 182-191.

Graham, J. H., Krzysik, A. J., Kovacic, D. A., Duda, J. J., Freeman, D. C., Emlen, J. M., ... & Balbach, H. E. (2009). Species richness, equitability, and abundance of ants in disturbed landscapes. *Ecological Indicators*, *9*(5), 866-877.

Guerra, E. E., Blanco, C. M., & Garrie, J. (2019). The impact of prescribed fire on moth assemblages in the Boston Mountains and Ozark Highlands, in Arkansas. *Journal of the Arkansas Academy of Science*, *73*(1), 31-38.

Gustafsson, L., Berglind, M., Granström, A., Grelle, A., Isacsson, G., Kjellander, P., ... & Mikusiński, G. (2019). Rapid ecological response and intensified knowledge accumulation following a north European mega-fire. Scandinavian Journal of Forest Research, 34(4), 234-253.

Habel, J. C., Segerer, A. H., Ulrich, W., & Schmitt, T. (2019). Succession matters: Community shifts in moths over three decades increases multifunctionality in intermediate successional stages. *Scientific Reports*, *9*(1), 5586.

Halkidi, M., Batistakis, Y., & Vazirgiannis, M. (2001). On clustering validation techniques. *Journal of intelligent information systems*, *17*, 107-145.

Harabiš, F., & Dolný, A. (2018). Military training areas as refuges for threatened dragonfly species: Effect of spatial isolation and military activity. *Biological Conservation*, *217*, 28-35.

Hennig, C., & Imports, M. A. S. S. (2015). Package ‘fpc’. *Flexible procedures for clustering*, *1176*.

Hejda, R., Farkač, J., & Chobot, K. (2017). Červený Seznam Ohrožených Druhů České Republiky: Bezobratli: Red List of Threatened Species of Czech Republic: Invertebrates. *Příroda*, 1-611.

Hilt, N., & Fiedler, K. (2005). Diversity and composition of Arctiidae moth ensembles along a successional gradient in the Ecuadorian Andes. *Diversity and Distributions*, *11*(5), 387-398.

Hilt, N., Brehm, G., & Fiedler, K. (2006). Diversity and ensemble composition of geometrid moths along a successional gradient in the Ecuadorian Andes. *Journal of tropical Ecology*, *22*(2), 155-166.

Horn, H. S. (1974). The ecology of secondary succession. *Annual review of ecology and systematics*, 25-37.

Højsgaard, S., Halekoh, U., Yan, J., & Ekstrøm, C. (2024). Package ‘geepack’. R package version, 1-2.

Hubl, E. (2019). Zrušení vojenského újezdu Brdy a založení CHKO Brdy.

Hughes, J. B. (2000). The scale of resource specialization and the distribution and abundance of lycaenid butterflies. *Oecologia*, *123*, 375-383.

Huston, M., & Smith, T. (1987). Plant succession: life history and competition. *The American Naturalist*, *130*(2), 168-198.

Jentsch, A., Friedrich, S., Steinlein, T., Beyschlag, W., & Nezadal, W. (2009). Assessing conservation action for substitution of missing dynamics on former military training areas in Central Europe. *Restoration Ecology*, *17*(1), 107-116.

Jirku, D., Hais, M., & Jirku, M. (2020). Osud vojenských prostorů: krajiny protékající mezi prsty [The fate of military areas: landscapes that seep through your fingers]. *Živa*, *2020*(5), 265-267.

Kassambara, A., & Mundt, F. (2017). Package ‘factoextra’. *Extract and visualize the results of multivariate data analyses*, *76*(2).

Kleyer, M., Dray, S., Bello, F., Lepš, J., Pakeman, R. J., Strauss, B., ... & Lavorel, S. (2012). Assessing species and community functional responses to environmental gradients: which multivariate methods?. *Journal of vegetation science*, *23*(5), 805-821.

Keeley, J. E. (2009). Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International journal of wildland fire*, *18*(1), 116-126.

Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in plant science*, *16*(8), 406-411.

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, *169*, 1043-1052.

Kirkpatrick, L., Mitchell, S. N., & Park, K. J. (2018). The metric matters when assessing diversity: Assessing lepidopteran species richness and diversity in two habitats under different disturbance regimes. *Ecology and Evolution*, *8*(22), 11134-11142.

Kitahara, M., Sei, K., & Fujii, K. (2000). Patterns in the structure of grassland butterfly communities along a gradient of human disturbance: further analysis based on the generalist/specialist concept. *Population Ecology*, *42*, 135-144.

Kral, K. C., Limb, R. F., Harmon, J. P., & Hovick, T. J. (2017). Arthropods and fire: Previous research shaping future conservation. Rangeland Ecology & Management, 70(5), 589-598.

Konvička, M., Beneš, J., & Čížek, L. (2005). *Ohrožený hmyz nelesních stanovišť: ochrana a management*. Sagittaria.

Kouki, J., Hyvärinen, E., Lappalainen, H., Martikainen, P., & Similä, M. (2012). Landscape context affects the success of habitat restoration: large-scale colonization patterns of saproxylic and fire-associated species in boreal forests. *Diversity and Distributions*, *18*(4), 348-355.

Laštůvka, Z.; Liška, J.; Šumpich, J. (2023). Motýli (Lepidoptera) Česka - aktualizovaný seznam druhů. Vyd. první. Brno: Mendelova univerzita v Brně. 108 s.

Legendre, P., R. Galzin, and M. L. Harmelin-Vivien. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. Ecology 78:547–562.

Lenth, R. V. (2024). *emmeans: Estimated marginal means, aka least-squares means* (R package version 1.10.2). Retrieved from https://cran.r-project.org/package=emmeans

Lentile, L. B., Holden, Z. A., Smith, A. M., Falkowski, M. J., Hudak, A. T., Morgan, P., ... & Benson, N. C. (2006). Remote sensing techniques to assess active fire characteristics and post-fire effects. *International Journal of Wildland Fire*, *15*(3), 319-345.

Lindenmayer, D. B., MacGregor, C., Wood, J., Westgate, M. J., Ikin, K., Foster, C., ... & Zentelis, R. (2016). Bombs, fire and biodiversity: Vertebrate fauna occurrence in areas subject to military training. *Biological Conservation*, *204*, 276-283.

Lintott, P. R., Bunnefeld, N., Fuentes-Montemayor, E., Minderman, J., Blackmore, L. M., Goulson, D., & Park, K. J. (2014). Moth species richness, abundance and diversity in fragmented urban woodlands: implications for conservation and management strategies. *Biodiversity and Conservation*, *23*, 2875-2901.

Lovegrove, A. T. (2017). *Management and monitoring in protected areas: a case study in the New Forest National Park. The effects upon Valley Mire and Heathland Communities* (Doctoral dissertation, Bournemouth University).

Macek, J., Dvorak, J., Traxler, L. & Cervenka, V. (2007) Motyli a housenky strednı Evropy: Nocnı motyli I, pp. 371. Academia, Praha.

Macek, J., Dvorak, J., Traxler, L. & Cervenka, V. (2008) Motyli a housenky strednı Evropy: Nocnı motyli II– Murovitı, pp. 492. Academia, Praha.

Macek, J., Prochazka, J. & Traxler, L. (2012) Motyli a housenky strednı Evropy: Nocnı motyli III- Pıd’alkovitı, pp. 424. Academia, Praha.

Mackey, R. L., & Currie, D. J. (2001). The diversity–disturbance relationship: is it generally strong and peaked?. *Ecology*, *82*(12), 3479-3492.

Mataix-Solera, J., Cerdà, A., Arcenegui, V., Jordán, A., & Zavala, L. M. (2011). Fire effects on soil aggregation: a review. *Earth-Science Reviews*, *109*(1-2), 44-60.

Merta, L., & Roleček, J. (2005). Vojenský výcvikový prostor Libavá-nová a ojedinělá lokalita žábronožky letní (Branchipus schaefferi Fischer, 1834) na Moravě. *Časopis Slezského muzea, série A, vědy přírodní*, (1).

Midgley, J. J., & Bond, W. J. (2013). Plant adaptations to fire: an evolutionary perspective. *Fire phenomena and the earth system: An interdisciplinary guide to fire science*, 125-134.

MO ČR, 2024. Informace o vojenských újezdech [online]. Praha MO ČR, s. p. [cit. 1. 11. 2024]. Dostupné z: https://acr.mo.gov.cz/scripts/detail.php?id=215

Moyo, S. (2022). Community Responses to Fire: A Global Meta-Analysis Unravels the Contrasting Responses of Fauna to Fire. *Earth*, *3*(4), 1087-1111.

New, T. R. (2023). Introducing Moth Variety and Diversity. In *The Other Lepidoptera: Moth Conservation in Australia* (pp. 1-20). Cham: Springer International Publishing.

Niemelä, P. (1983, January). Seasonal patterns in the incidence of specialism: Macrolepidopteran larvae on Finnish deciduous trees. In *Annales Zoologici Fennici* (pp. 199-202). Finnish Academy of Sciences, Societas Scientiarum Fennica, Societas pro Fauna et Flora Fennica and Societas Biologica Fennica Vanamo.

Nowacki, J., & Pałka, K. (2015). Noctuid moths (Lepidoptera: Noctuoidea: Nolidae, Erebidae, Noctuidae) of the Nowa Dęba Military Training Area in the Sandomierz Primeval Forest (south-eastern Poland). *Fragmenta Faunistica*, *58*(1), 21-36.

Odum, E. P. (1969). The Strategy of Ecosystem Development: An understanding of ecological succession provides a basis for resolving man's conflict with nature. *science*, *164*(3877), 262-270.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'hara, R. B., ... & Oksanen, M. J. (2013). Package 'vegan'. *Community ecology package, version*, *2*(9), 1-295.

Palivcová, L. (2018). Vliv činnosti armády na sukcesi společenstev terestrických členovců v CHKO Brdy.

Pavlikova, A., & Konvicka, M. (2012). An ecological classification of Central European macromoths: habitat associations and conservation status returned from life history attributes. *Journal of Insect Conservation*, *16*, 187-206.

Pešout, P. (2021). Legalizace vypalování porostů v ČR. Dostupné také z: http://knihovna.geology.cz/Carmen/cs/detail/42513.

Potocký, P., Bartoňová, A., Beneš, J., Zapletal, M., & Konvička, M. (2018). Life-history traits of Central European moths: gradients of variation and their association with rarity and threats. *Insect Conservation and Diversity*, *11*(5), 493-505.

Rákosy, L. & Schmitt, T. (2011) Are butterflies and moths suitable ecological indicator systems for restoration measures of semi-natural calcareous grassland habitats? Ecological Indicators, 11, 1040 1045

Reif, J., Marhoul, P., Čížek, O., & Konvička, M. (2011). Abandoned military training sites are an overlooked refuge for at-risk open habitat bird species. *Biodiversity and Conservation*, *20*, 3645-3662.

R Core Team (2016): R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Romme, W. H. (1982). Fire and landscape diversity in subalpine forests of Yellowstone National Park. *Ecological Monographs*, *52*(2), 199-221.

Rosa García, R., Fraser, M. D., Celaya, R., Ferreira, L. M. M., García, U., & Osoro, K. (2013). Grazing land management and biodiversity in the Atlantic European heathlands: a review. *Agroforestry Systems*, *87*, 19-43.

Rousseeuw, P. J. (1987). Silhouettes: a graphical aid to the interpretation and validation of cluster analysis. *Journal of computational and applied mathematics*, *20*, 53-65.

Scott, J. H. (2001). *Assessing crown fire potential by linking models of surface and crown fire behavior* (No. 29). US Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sedláček, O., & Marhoul, P. (2016). Hoří, má panenko. *Minulost a budoucnost ohně (nejen) v Brdech, Fórum ochrany přírody, roč*, *3*, 34-36.

Sedláček, O., Marhoul P., Dušek J. (2015): Využití řízených požárů v ochranářském managementu se zvláštním zřetelem na jeho využití při managementu bezlesí navrhované CHKO Brdy. Nepubl. studie zpracovaná pro AOPK ČR. 122 pp.

Sedláková, I., & Chytrý, M. (1999). Regeneration patterns in a Central European dry heathland: effects of burning, sod-cutting and cutting. *Plant Ecology*, *143*, 77-87.

Seifert, C. L., Strutzenberger, P., & Fiedler, K. (2023). How do host plant use and seasonal life cycle relate to insect body size: A case study on European geometrid moths (Lepidoptera: Geometridae). *Journal of Evolutionary Biology*, *36*(5), 743-752.

Schaeffer, E. (2013). *The short-term effects of a high severity forest fire on moth communities in New Mexico* (Doctoral dissertation, University of the South).

Schernhammer, T., Wessely, J., Eder, E., Straka, U., & Essl, F. (2020). Modelling the distribution of large branchiopods (Crustacea: Notostraca, Anostraca & Spinicaudata) for predicting occurrences in poorly sampled regions. *Global Ecology and Conservation*, *23*, e01083.

Shewring, M. P., Vaughan, I. P., & Thomas, R. J. (2022). Moth biomass and diversity in coniferous plantation woodlands. *Forest Ecology and Management*, *505*, 119881.

Slavík, B. (1988). *Květena České socialistické republiky: Dl. 1*. Academia.

Šíblová, Z., Lehotská, B., & Moyzeová, M. (2021). THE IMPACT OF MILITARY TRAINING-RELATED DISTURBANCES IN ZÁHORIE MILITARY TRAINING AREA (WESTERN SLOVAKIA) ON THE DRAGONFLIES DIVERSITY. *Studia Universitatis Vasile Goldis Seria Stiintele Vietii (Life Sciences Series)*, *31*(3).

Sobek, S., Scherber, C., Steffan-Dewenter, I., & Tscharntke, T. (2009). Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany's largest connected deciduous forest. *Oecologia*, *160*, 279-288.

Steel, Z. L., Safford, H. D., & Viers, J. H. (2015). The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere*, *6*(1), 1-23.

Summerville, K. S., Ritter, L. M., & Crist, T. O. (2004). Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biological Conservation*, *116*(1), 9-18.

Summerville, K. S., Wilson, T. D., Veech, J. A., & Crist, T. O. (2006). Do body size and diet breadth affect partitioning of species diversity? A test with forest Lepidoptera. *Diversity and Distributions*, *12*(1), 91-99.

Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., ... & Swanson, F. J. (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, *9*(2), 117-125.

Tagarev, T. (2004). "From downsizing to modernising defence in C&E Europe: opportunities for SME's," in Defence related SME's: analysis and description of current conditions. Editor F. D. Carvalho (Amsterdam: NATO advanced science institutes series).

Thom, M. D., Daniels, J. C., Kobziar, L. N., & Colburn, J. R. (2015). Can butterflies evade fire? Pupa location and heat tolerance in fire prone habitats of Florida. PLoS One, 10(5), e0126755.

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833-2849.

Uhl, B., Wölfling, M., & Fiedler, K. (2021). Qualitative and quantitative loss of habitat at different spatial scales affects functional moth diversity. *Frontiers in Ecology and Evolution*, *9*, 637371.

Valkó, O., Török, P., Deák, B., & Tóthmérész, B. (2014). Prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic and applied Ecology*, *15*(1), 26-33.

van Asch, M., & Visser, M. E. (2007). Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annu. Rev. Entomol.*, *52*(1), 37-55.

Velle, L. G., Nilsen, L. S., Norderhaug, A., & Vandvik, V. (2014). Does prescribed burning result in biotic homogenization of coastal heathlands?. *Global Change Biology*, *20*(5), 1429-1440.

Viedma, O., Meliá, J., Segarra, D., & Garcia-Haro, J. (1997). Modeling rates of ecosystem recovery after fires by using Landsat TM data. *Remote Sensing of Environment*, *61*(3), 383-398.

VLS ČR, 2024. Historie podniku [online]. Praha: VLS ČR, s. p. [cit. 1. 11. 2024]. Dostupné z: https://www.vls.cz/o-vls/historie-podniku

Voska, V. (2018). Vliv vojenské činnosti na diverzitu a výskyt plazů v CHKO Brdy.

Walker, L. R., & Del Moral, R. (2003). *Primary succession and ecosystem rehabilitation*. Cambridge University Press.

Walczak, U. (2011). Leaf-mining moths (Lepidoptera) of the Biedrusko military area in western Poland. *Fragmenta Faunistica*, *54*(2), 113-136.

Walter, J., Bartoňová, A. S., & Fric, Z. F. (2022). The impact of a forest fire event on moth assemblages in Western Bohemia, Czech Republic. *Polish Journal of Ecology*, *69*(3-4), 156-171.

Warren, S. D., Holbrook, S. W., Dale, D. A., Whelan, N. L., Elyn, M., Grimm, W., & Jentsch, A. (2007). Biodiversity and the heterogeneous disturbance regime on military training lands. *Restoration Ecology*, *15*(4), 606-612.

Warren, S. D., & Büttner, R. (2008a). Relationship of endangered amphibians to landscape disturbance. *The Journal of Wildlife Management*, *72*(3), 738-744.

Warren, S. D., & Büttner, R. (2008b). Active military training areas as refugia for disturbance-dependent endangered insects. *Journal of Insect Conservation*, *12*, 671-676.

Wei, T., Simko, V. R., Levy, M., Xie, Y., Jin, Y., & Zemla, J. (2021). package “corrplot”: Visualization of a Correlation Matrix. 2017. *Version 0.84*.

White, P. S., and S. T. A. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. Pages 3–13 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Wikars, L. O. (1992). Skogsbrander och insekter. Entomol. tidskr, 113, 1-12.

Wikars, L. O. (2002). Dependence on fire in wood-living insects: an experiment with burned and unburned spruce and birch logs. Journal of Insect Conservation, 6(1), 1-12.

Wickham, H., Chang, W., & Wickham, M. H. (2016). Package ‘ggplot2’. *Create elegant data visualisations using the grammar of graphics. Version*, *2*(1), 1-189.

Wölfling, M., Uhl, B., & Fiedler, K. (2019). Multi-decadal surveys in a Mediterranean forest reserve–do succession and isolation drive moth species richness?. *Nature Conservation*, *35*, 25-40.

Zografou, K., Swartz, M. T., Tilden, V. P., McKinney, E. N., Eckenrode, J. A., & Sewall, B. J. (2017). Severe decline and partial recovery of a rare butterfly on an active military training area. *Biological Conservation*, *216*, 43-50.