

Charles University

Faculty of Science

Study programme: Biology

Study specialisation: Geobotany



Bc. Karolína Hrušková

Population dynamics of *Minuartia smejkalii*

Populační dynamiku kuřičky hadcové (*Minuartia smejkalii*)

Diploma thesis

Supervisor: prof. RNDr. Zuzana Münzbergová, Ph.D.

Consultant: RNDr. Hana Pánková, Ph.D.

Praha, 2021

Prohlášení

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

V Praze dne 26. 4. 2021

Podpis

Karolína Hrušková

Acknowledgment

First, I would like to thank my supervisor Zuzana Münzbergová for her valuable advice, help and patience in solving all my not only technical problems. I would also like to thank Eelke Jongejans very much for revealing the magic of IPM and teaching me how to use this method to analyses my data. Thank you for the beautiful 2 months in Netherlands where it felt like home and for your patience with explaining me all of the statistical techniques. Additional thanks goes to Hana Pánková, who taught me all the work in the field and for a friendly environment and involvement in the Life project. Without Hanka, there would be no *Minuartia smejkalii*.

I would like to thank my whole family and my partner Ivan Slyvka, who supported me during the whole time. I am thankful for the help in making the monitoring squares, renting a car, preparing field snacks, motivation and strength for collecting data and writing this thesis. Additionally, I would also like to thank the fire brigade of the city of Kolín, namely Vlastimil Soukup, for lending the fishing trousers. Finally, I thank all my friends, classmates and students from the Otevřená věda project who participated in data collection or helped me with the angry R code.

As part of this thesis, there was a two-month internship in the Netherlands at Radboud University in Nijmegen. The internship was undertaken with the support of the Fond Mobility of the Faculty of Science, Charles University. The contribution was provided on proposal number: FM / c / 2020-X-007. Further support for the internship was provided by the Podpora Internacionalizace of the Faculty of Science of Charles University as co-financing of the above-mentioned application in the Fond Mobility. Without the support of the two funds mentioned above, it would not be possible to carry out an internship.

The study was supported by Project LIFE for *Minuartia* (Grant No. LIFE15NAT/CZ/000818), which is implemented with the financial contribution of the European Union, the Life program and with the financial contribution of the Ministry of Environment of the Czech Republic.

In conclusion, I would like to thank everyone who is interested in reading my thesis, because it takes a great deal of strength and courage to understand the issue of IPM.

"Love begins with a comparison from botany and ends with a comparison from zoology." -

Eugene Labiche (1815 - 1888)

Abstrakt

Hadcové oblasti tvoří v krajině významné ostrůvky se specifickými chemickými vlastnostmi. Na území České republiky nalezneme jen málo oblastí s hadcovým podložím a vegetací, která se na tomto specifickém podloží vyskytuje. Nejvýznamnější vlastností, kterou se hadce odlišují od okolních hornin, je vysoký obsah hořčíku a jiných těžkých kovů. Vzhledem k této vlastnosti je hadcová hornina pro většinu rostlin toxická a znemožňuje jim zde jejich výskyt. Současně tato vlastnost přispívá ke vzniku hadcových specialistů, kteří hadcové podloží naopak vyhledávají. Zvýšené nároky na přežívání a výskyt rostlin vedou ke vzniku endemických druhů obligátně specializovaných na tato stanoviště. Jedním z předních hadcových specialistů s endemickým výskytem v České republice je kuřička hadcová (*Minuartia smejkalii*).

V současné době jsou hadcové lokality ohrožovány postupným zarůstáním lokalit, nedostatečným či špatným managementem lokalit, překrýváním hadcových výchozů nadbytečným opadem a humusovou vrstvou a v poslední řadě i fragmentací a zmenšováním lokalit v důsledku antropogenních aktivit. Společně se zanikajícími lokalitami tak z krajiny mizí i hadcový specialista, kterým je i již výše zmíněná kuřička hadcová.

Cílem této diplomové práce bylo provést důkladný monitoring lokalit s výskytem tohoto druhu, sběr populačních, stanovištních a klimatických dat, aby bylo možné definovat životní cyklus endemické rostliny rozvolněných hadcových borů a faktory, které její životní cyklus ovlivňují. K tomuto cíli byla nashromážděna data ze 7 populací. Data pokrývají monitorovací období od roku 2006 do roku 2020. Vhodnou statistickou metodou pro analýzy byla zvolena metoda Integral projection models (IPMs). IPM umožňuje propojit data o klimatu a stanovišti s daty o populační dynamice druhu.

Výsledkem této diplomové je Integral projection model, který odhalil výrazný vliv klonálního rozmnožování na populační dynamiku *M. smejkalii*. Největší vliv na populační dynamiku na základě IPM má přežívání jedinců. Významnou roli v životním cyklu *M. smejkalii* hrají velcí kvetoucí jedinci, velcí nekvetoucí jedinci, semena a zejména semenná banka. Po přidání klimatických a stanovištních faktorů do modelů popisujících vital rates nedošlo k prokázání žádného vlivu na populační dynamiku *M. smejkalii*. Na základě těchto výsledků nedošlo k přidání klimatických a stanovištních podmínek do finálního IPM.

Managementy aplikované na lokalitách od roku 2016 pravděpodobně způsobily nárůst počtu jedinců na lokalitách. Ovšem tato hypotéza nebyla zatím potvrzena za pomoci modelů vital rates ani IPM. Jejich vliv bude nutné prověřit další studií.

Klíčová slova: hadec, *Minuartia smejkalii*, Integral Projection models, populační dynamika, klima, abiotické podmínky, management

Abstract

Serpentine areas in the Czech Republic form minor but important islands in the landscape with specific chemical properties such as high content of magnesium and other heavy metals. Due to this, serpentine is toxic for most plants. Increased demands on the survival and occurrence of plants lead to the emergence of serpentine specialists obligatorily specialized in these extreme habitats.

Currently, serpentine areas are threatened by gradual overgrowth of sites, insufficient or poor site management and fragmentation or shrinkage of sites due to anthropogenic activities. Along with the disappearing localities, the serpentine specialists, are becoming highly endangered. *Minuartia smejkalii* is highly endangered serpentine specialist with an endemic occurrence in the Czech Republic with great need of its conservation.

The aim of the work was to collect data on population dynamics of the species and identify habitat and climatic factors affecting population growth. We studied dynamics in all existing 7 populations during the period from 2006 to 2020 were collected. We linked these data to information on population dynamics, habitat and climatic factors and analysed them using Integral projection models (IPM).

The study presents the importance of individual habitat and climatic conditions on the dynamics of *M. smejkalii*. It will also try to estimate the development of the population dynamic during climate change and propose a suitable management not only for this endemic species, but for the entire eminent serpentine habitat of the Czech Republic.

The result of this diploma is the Integral projection model, which revealed a significant effect of clonal reproduction on the population dynamics of *M. smejkalii*. Based on IPM, the survival of individuals has the greatest influence on population dynamics. Large flowering individuals, large non-flowering individuals, seeds and the seed bank play an important role in the life cycle of *M. smejkalii*. The addition of climatic and habitat factors to the models describing vital rates did not show any effect on the population dynamics of *M. smejkalii*. Based on these results, climatic and habitat conditions were not added to the final IPM.

Management applied at localities since 2016 has probably caused an increase in the number of individuals at localities. However, this hypothesis could not be verified using vital rates or IPM models. Their effect will have to be examined in further studies.

Key words: serpentine, *Minuartia smejkalii*, Integral Projection models, population dynamics, climate, abiotic conditions, management

Contents

1	Introduction	4
2	Methodology	6
2.1	Species <i>Minuartia smejkalii</i>	6
2.2	Serpentine	7
2.2.1	Properties of serpentine	7
2.2.2	Serpentine areas in Czech Republic	7
2.2.3	Study area and sites	8
2.2.3.1	Hadce u Želivky National Natural Monument	9
2.2.3.2	Hadce u Hrnčír Natural Monument	12
2.3	Population data	13
2.3.1	Data collection	13
2.3.1.1	Number of flowers per capsule	14
2.3.1.2	Seeds per capsule	15
2.3.1.3	Seed bank	16
2.3.1.4	Sowing experiment	17
2.4	Climatic data	17
2.5	Habitat data	19
2.6	Management of localities	19
2.7	Data analysis	20
2.7.1	Creation of integral projection models	21
3	Results	22
3.1	Life cycle of <i>Minuartia smejkalii</i>	22
3.2	Dataset diagnostics and construction of Integral projection models for <i>M. smejkalii</i>	23
3.2.1	Selection of suitable models and parameters for IPM	23
3.2.2	Number of individuals of <i>M. smejkalii</i> between years 2005-2020	26
3.2.3	The size of <i>M. smejkalii</i> individuals	27
3.2.3.1	Relationship between the size of <i>M. smejkalii</i> individuals in year t and in year $t + 1$	28
3.2.4	Vegetative and flowering individuals in the life cycle of <i>Minuartia smejkalii</i>	28
3.2.4.1	Probability of flowering and proportion of flowering in the next year $t+1$	30

3.2.5	Dry plants in the life cycle of <i>Minuartia smejkalii</i>	32
3.2.6	Dormant individuals in the life cycle of <i>Minuartia smejkalii</i>	33
3.2.7	Clonal propagation by the disintegration of tufts of <i>Minuartia smejkalii</i> .	35
3.2.8	Seedlings and their fate in the life cycle of <i>Minuartia smejkalii</i>	36
3.2.9	Seed production in the life cycle of <i>Minuartia smejkalii</i>	37
3.2.10	Seed bank.....	38
3.3	Influence of climatic and habitat conditions.....	39
3.4	Evaluation of population dynamics of <i>Minuartia smejkalii</i> using IPM	41
4	Discussion	45
4.1	Missing data in the dataset.....	45
4.2	Seed production, germination and seed bank	45
4.3	Sowing experiment.....	46
4.4	Influence of climatic and habitat conditions on vital rates	46
4.5	Result of integral projection models	47
5	Conclusion	49
6	References.....	50

List of Abbreviations

Abbreviations:	Meaning:
IPM	Integral projection model
GLA	Gap light analyzer
BIC	Bayesian information criterion
LMER	Linear mixed effects model
GLMER	Generalizes linear mixed-effects model
IUCN	International Union for Conservation of Nature

1 Introduction

Serpentine is a rare type of bedrock that occurs in the landscape only very rarely. It is a bedrock with extremely stressful living conditions for plant species (Anacker, 2014). It is an ultrabasic bedrock with a high content of magnesium, heavy metals and low calcium content. These chemical properties can be toxic to many plant species. Other specificities of serpentines are high temperature fluctuations of the soil surface, frequent lack of water and shallow soil horizon. These conditions contribute to the frequent emergence of serpentine specialists with a high proportion of endemic species (Brady et al., 2005). Serpentine “islands” thus become important habitats with a high diversity of plant species (Anacker et al., 2011).

Currently, this type of habitat is affected by the negative influences which leads to the disappearance of these rare habitats. Disappearance of serpentine habitats leads to loss in serpentine specialists. The loss of serpentine specialists leads to a reduction of the biodiversity of our landscape. Factors negatively affecting serpentine habitats are: overgrowing of localities with pioneer trees, overlapping of serpentine outcrops with humus layer (Pánková, 2011), change in climatic conditions (Damschen et al., 2012) and finally anthropogenic activities such as mining and fragmentation of habitats (Pešout, 2001).

Minuartia smejkalii is a leading serpentine specialist which is negatively affected by habitat reduction and fragmentation. It is a Czech endemic species occurring in only two localities, namely Hadce u Želivky National Natural Monument and Hadce u Hrnčír Natural Monument. The species survives here in a loose pine forest on serpentine rock outcrops (Hejný and Slavík, 1990). In the surrounding vegetation are presented other important species such as *Asplenium cuneifolium* and *Potentilla crantzii subsp. serpentini* (Chytrý et al., 2010).

Due to unfavorable conditions (for example fragmentation and overgrowing of localities) an initial degradation of the rare serpentine area started between years 1965 – 1975 (Pešout, 2001). This degradation has caused a decrease in the number of species occurring in the area. Therefore, it was necessary to assess the state of populations of rare plant species in localities and determine the appropriate management of habitats. The main species requiring stabilization of population growth was *Minuartia smejkalii*. To be able to assess the state of localities and the state of the populations of *Minuartia smejkalii*, monitoring of this species started in 2006. At the localities population, climatic, but also habitat data were collected.

This diploma thesis focuses on the evaluation of the population dynamics of the endemic species *Minuartia smejkalii* in the years 2006 - 2020. The thesis aims to define the life cycle of *Minuartia smejkalii* and use Integral projection models (IPM) to determine the population growth rate of the species. It will also be possible to use climatic and habitat data and link them with the vital rates analysis.

Based on previous studies of the species *M. smejkalii* the use of generally more commonly used matrix projection models seems inappropriate (Pánková, 2011). Matrix projection models work with a population divided into discrete units (Caswell, 2001). However, there are populations where the individual is characterized by a continuous variable, such as size. For this purpose, Integral projection models (IPM) are used in population biology. IPMs are an alternative to matrix projection models (Rees et al., 2014) and their use in the case of *M. smejkalii* will be more appropriate.

IPM offers the possibility of linking population, climatic and habitat data. Using IPM, it will be possible to define factors influencing the population dynamics of *M. smejkalii*. Defining these factors will help to create the suitable management plans that will positively affect the occurrence of this endemic species in the landscape and will also help to stabilize the rare serpentine localities of the Czech Republic.

Questions:

1. What is the population dynamics of the endemic species *Minuartia smejkalii*?
2. Which stages in the life cycle of *Minuartia smejkalii* most influence population dynamics?
3. What are the main factors and how do they affect the population dynamics of *Minuartia smejkalii*?
4. What management measures will help keep the species in the landscape and stop the degradation of an important serpentine habitat?

2 Methodology

2.1 Species *Minuartia smejkalii*

Minuartia smejkalii (Dvořáková) is a species of the *Caryophyllaceae* family. It is an endemic plant of the Czech Republic occurring on a serpentine substrate (Dvořáková, 1988). The plant was first determined as a separate species based on pollen analysis by Dvořáková (1988). Stojanova et al. (2020) showed genetic difference of *M. smejkalii* from the related species *M. caespitosa* and *M. corcontica*. *Minuartia smejkalii* is likely a glacial relict from the time when *Minuartia verna* agg. descended during the last glacial maximum into the so-called interglacial refuges. Based on the isolation in these refuges and as a result of stress factors acting on the serpentine substrate, the species became genetically isolated (Stojanova et al., 2020).

Minuartia smejkalii belongs to the species of priority European interest according to Habitats directive 92/43/EEC (Annex II) by the IUCN (Bilz et al., 2011). Within the Czech Republic, the species is classified as a critically endangered species (C1r) protected by law (No. 395/1992) (Grulich and Chobot, 2017). The species occurs in two localities in Czech Republic which are vicinity of Dolní Kralovice and vicinity of Mladá Vožice (Hejný and Slavík, 1990).

Minuartia smejkalii is a perennial plant growing in loose pine forests on rocky slopes and in rock crevices. It is a bushy plant with densely leafed sterile stems and 8-15 cm tall fertile stems with 3-12 flowers. The flowers are white and tiny (diameter up to 4 mm). The fruit is capsules containing asymmetrical kidney-shaped seeds up to 0.6 mm in diameter. The seeds do not have a smooth surface, but they are covered with papillae (Hejný and Slavík, 1990).

The main vegetation type typical for the occurrence of *M. smejkalii* is the Peri-Alpidic serpentine pine forest. It is a vegetation type with a very sparse representation in the Czech Republic (Chytrý et al., 2010). Since 1960, localities have been dramatically affected by anthropogenic activity. The sites were partially flooded by the creation of a water reservoir, partially excavated and further fragmented by the creation and widening of the D1 motorway (Pešout, 2001).



Fig. 1 One individual of *Minuartia smejkalii* on serpentine rock in locality Hadce u Želivky National Natural Monument, photograph Karolína Hrušková 2019

2.2 Serpentine

2.2.1 Properties of serpentine

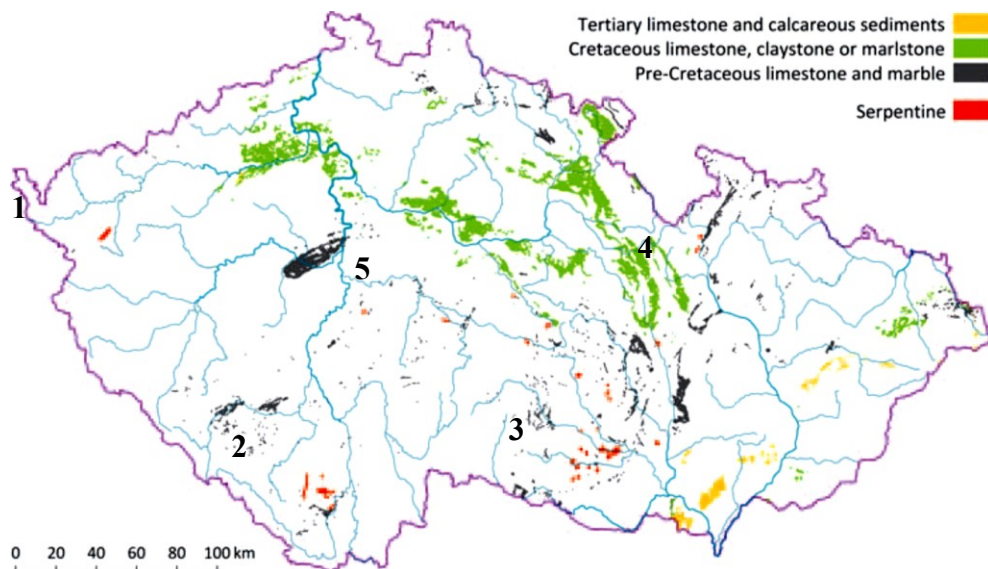
Serpentines are ubiquitous, but patchily distributed all around the world. They host different vegetation from the surrounding landscape with low plant productivity and a high degree of endemism (Brady et al., 2005). The specific vegetation on the serpentine is given mainly by its chemical and physical properties. It is a metamorphic rock that is rich in magnesium and heavy metals (such as iron, nickel, chromium, and cobalt). Excess of magnesium causes low concentrations of calcium and other elements such as nitrogen, potassium, and phosphorus (Brady et al., 2005; Damschen et al., 2012). The rock is prone to erosion and differs in its water and temperature regime. The soils developing on serpentines are toxic to most plant species. Furthermore, specific temperature and water regimes cause additional stress for plants and are limiting factors for plant growth. All these conditions help to create serpentine specialists adapted to the demanding conditions prevailing in this environment (Anacker, 2014; Harrison et al., 2006).

2.2.2 Serpentine areas in Czech Republic

Serpentine areas in the Czech Republic are located mainly in the western and southwestern part of the Bohemian Massif, in the area of the Czech-Moravian Highlands and

in northern Moravia. The distribution of serpentines areas in the Czech Republic is shown on *Map 1* taken from Chytrý et al. (2013). Due to the shallow soil horizon and frequent rocky outcrops subject to erosion, the serpentines are covered with open pine forests. These places are often the site of glacial relics or neoendemites, such as *Cerastium alsinifolium* and *Minuartia smejkalii* (Chytrý et al., 2013).

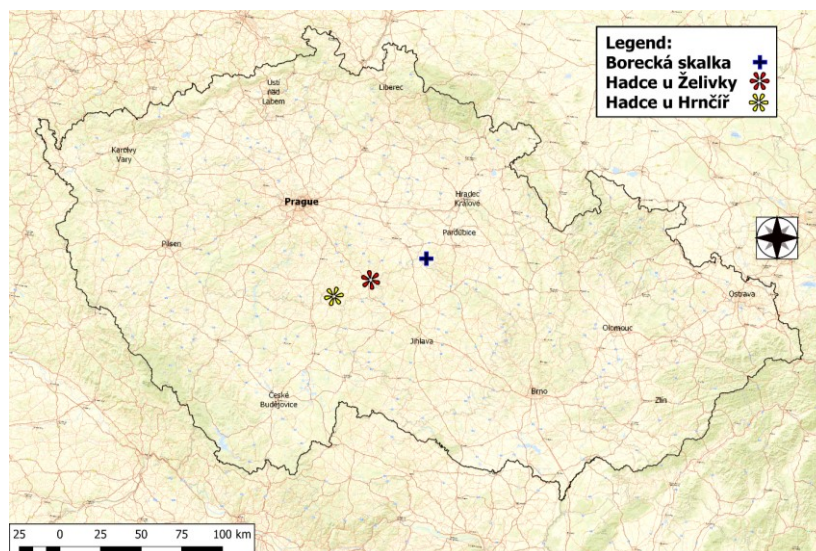
The most important serpentines areas in the Czech Republic include the Slavkovský les Mountains (western Bohemia), the area around the town of Křemže (southern Bohemia), the Mohelenská hadcová steppe (south-western Moravia), surroundings of the village Raškov (northern Moravia) and finally the slopes around the Želivka reservoir (central Bohemia). Location of important serpentine areas are marked in *Map 1*. (Chytrý et al., 2013).



Map 1 Distribution of serpentines areas in the Czech Republic is shown by red colour (based on digital geological map of the Czech Republic 1 : 50,000 by Czech Geological Survey 2004). The numbers show the most important serpentine areas in the Czech Republic. 1 – Slavkovský les Mountains, 2 – Křemže, 3- Mohelenská hadcová steppe, 4- Raškov and 5 – Serpentine area Želivka. Taken from Chytrý et al., 2013, edited by K. Hrušková 2021

2.2.3 Study area and sites

Minuartia smejkalii occurs in two localities in the vicinity of Dolní Kralovice in Hadce u Želivky National Natural Monument and in the second locality in vicinity of Mladá Vožice in Hadce u Hrnčář Natural Monument. The total area of these two localities with the occurrence of *M. smejkalii* is approximately 500 km². Previously, the species also occurred on the Borecká skalka Natural Monument. Unfortunately, the species went extinct in the 1960s as a result of mining work in the vicinity of the locality (Hejný and Slavík, 1990; Stojanova et al., 2020). Below is a *Map 2* showing known localities of *M. smejkalii*.



Map 2 Map of locality of *Minuartia smejkalii*. Monitoring of population dynamic of this species is realized on localities Hadce u Želivky (red symbol) and Hadce u Hrnčír (yellow symbol). On the last locality Borecká skalka (blue symbol) the species went extinct. Map from QGIS Desktop 3.8.3. Background map ESRI Standard, Karolína Hrušková 2020

2.2.3.1 Hadce u Želivky National Natural Monument

Hadce u Želivky is a locality situated in the Central Bohemian Region in the Benešov district (49.6888 °N, 15.1069 °E - WGS84). The vegetation at the site corresponds to the Peri-Alpidic serpentine pine forests (Fig. 2 and 3). It is the locality rich in the occurrence of rocky serpentine outcrops, which are overgrown with open pine forest. *Festuca ovina* and *Galium verum* are commonly represented in the herbaceous layer. The soil horizon is shallow, the terrain is sloping towards the reservoir. (Chytrý et al., 2010). Other rare species of vascular plants occurring in the area see Table 1

Hadce u Želivky		
Species	Threats according to Czech Republic	Threats according to IUCN
<i>Myosotis stenophylla</i>	C1r	EN
<i>Thlaspi montanum</i>	C3	NT
<i>Sesleria caerulea</i>	C2r	VU
<i>Asplenium cuneifolium</i>	C2r	VU
<i>Potentilla crantzii</i> subsp. <i>serpentini</i>	C1r	EN
<i>Thymus praecox</i>	C4a	LC

Taken over and edited from Grulich and Chobot, 2017

Table 1 Other important species of vascular plants occurring at the locality Hadce u Želivky together with *M. smejkalii*.



Fig. 2 Locality Hadce u Želivky, Site B2 (Bernartice 2). Photograph Karolína Hrušková 2019



Fig. 3 Locality Hadce u Želivky, Site DK 2 (Dolní Kralovice 2). Photograph Karolína Hrušková 2020

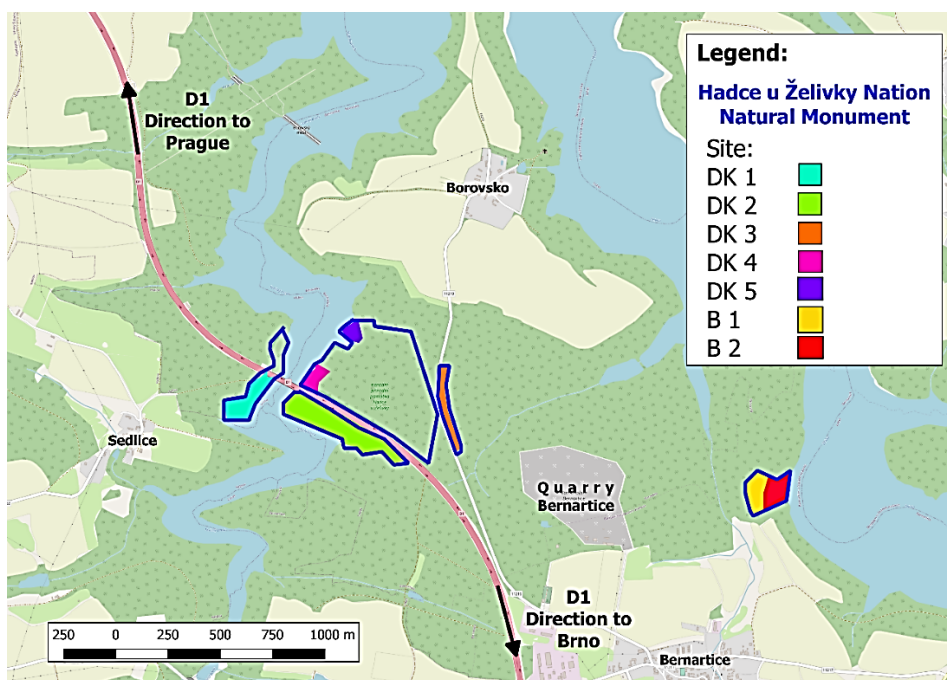
At the locality moss layer with dominants *Hylocomium splendens* and *Pleurozium schreberi* is also common (Chytrý et al., 2010). There are occasional landslides of material from the slope, especially the release of stones, rocks, and sludge. Litter is formed mainly by pine

needles and in some places, it forms very thick layers on the locality (Personal observation K. Hrušková, H. Pánková).

In order to define precise climatic and habitat conditions to create more accurate statistical models, the locality was divided on the basis of relief and occurrence of *M. smejkalii* into 7 sites. These habitats were further divided into 45 smaller microhabitats. One microhabitat is defined by one rock with *M. smejkalii* and identical habitat condition (see *Table 2* and *Map 3*). At the level of microhabitats data on soil properties, water capacity, shade and vegetation were collected. All parameters measured in this way at the level of microhabitat are further elaborated in the *Chapter 2. 4* and *2. 5*.

Locality	Sites	Number of Microhabitats
Hadce u Želivky	B1	16
	B2	1
	DK1	4
	DK2	14
	DK3	3
	DK4	4
Hadce u Hrnčič	H	16

Table 2 Overview of the division of the Hadce u Želivky and Hadce u Hrnčič localities into smaller units (site, microhabitats). B - Bernartice, DK - Dolní Kralovice and H - Hrnčiče



Map 3 Division of locality Hadce u Želivky (Border of Hadce u Želivky National Natural Monument are in blue colour). Locality is divided in to 7 sites, each of site is in the map marked by different colour. Map from QGIS Desktop 3.8.3. Background map OSM Standard, Karolína Hrušková 2020

2.2.3.2 Hadce u Hrnčič Natural Monument

Hadce u Hrnčič Natural Monument is situated in the Central Bohemian Region on the border with the South Bohemian Region in the Benešov District (49.5853 °N, 14.8511°E - WGS84). The locality is different in its vegetation type from the locality Hadce u Želivky. The vegetation at this locality belongs to the Boreo-continental pine forests type. It is a flatter locality in comparison with the locality of Hadce u Želivky and the serpentine rocks are less exposed. The locality is partly overgrown with spruce forest and is divided into two parts by a forest path, which is lined with acidophilic grass communities (See Fig. 4). The most common species in the herbaceous layer are: *Avenella flexulosa*, *Festuca ovina* and *Luzula luzuloides* subsp. *luzuloides*. Especially along the forest road often occurs *Molinia caerulea* agg., *Agrostis capillaris*, *Thymus pulegioides*, *Lychnis viscaria*, *Polygala vulgaris*, *Galium verum*, *Luzula campestris* agg. Together with *M. smejkalii* on locality there are species such as *Pinus sylvestris*, *Frangula alnus*, *Calluna vulgaris*, *Vaccinium myrtillus* and endangered but typical species of serpentine *Asplenium cuneifolium*. *Asplenium cuneifolium* is in Bohemia highly endangered species, according to the IUCN classified as vulnerable taxon (Grulich and Chobot, 2017). The moss layer contains mainly *Dicranium scoparium*, *Leucobryum glaucum* and *Pleurozium schreberii*. Based on the terrain and the occurrence of *M. smejkalii*, we divided Hadce u Hrnčič into 16 microhabitats (see Table 2 above) for which we obtained the habitat, climatic and population data as in the case of microhabitats at Hadce u Želivky.



Fig. 4 Locality Hadce u Hrnčič. Photograph Karolína Hrušková 2020

2.3 Population data

2.3.1 Data collection

In 2003, monitoring of some sites began. Data collection in the period 2003-2016 was performed by Hana Pánková. I joined to data collection in the year 2017. Since 2017 with the help of Hana Pánková I have been collecting population data of *M. smejkalii* and helping to collect climatic and habitat data. At first, only DK 2 site and part of the habitats at the Hadce u Hrnčír locality were mapped. Since 2006, monitoring has been extended to all sites monitored today which means 61 microhabitats. For a detailed overview, see *Table 2* (above). The species is monitored once a year during the period when *M. smejkalii* blooms and forms capsules with seeds. It is period between second half of May and the first half of July.

Monitoring was carried out from 2006 to 2020. During this period, monitoring was not carried out only in 2013 and in 2012 monitoring took place only at the locality Hadce u Hrnčír. The year 2013 was therefore omitted from the analyses. The missing year 2012 was averaged for the locality Hadce u Želivky from years 2011 and 2014. For individuals living in both years (2011 and 2014) the size was averaged. The number of new seedlings from this locality from year 2012 is unknown.

At the beginning of the monitoring, permanent squares (measuring 1×1 meter or 0.5 ×0.5 meter) in the places of occurrence of *M. smejkalii* were marked on each microhabitat. The size of the permanent square depended on the number of *M. smejkalii* individuals occurring in the area and on the terrain fragmentation (for example, the shape of a serpentine outcrop). The squares were marked with nails with colored plastic lids. Permanent squares facilitate plant monitoring and thanks to them, it is possible to accurately trace the position of individual plants.

The position of each individual *M. smejkalii* was recorded on a map corresponding to the dimensions and position of the permanent squares. Individuals of *M. smejkalii* were also marked with plastic tags with number (See *Fig. 5*), formerly metal tags with number. Every individual was then measured to calculate the area of the plant. For the calculation, the longest tuft length and the perpendicular tuft width were measured. The measured dimensions shown directly on the *M. smejkalii* individual are shown in *Fig. 5*. Based on the following measured dimensions, the area of the tuft was calculated for each plant according to the formula for calculating the area of the ellipse: $S = \pi \times (a/2) \times (b/2)$.

Another characteristic of the plants measured during monitoring was the number of flowering and non-flowering stems. Based on the knowledge of the number of flowering and non-flowering stems, it was possible to calculate the proportion of flowering of individual plants. The proportion of flowering means representation of the flowering stems within the whole plant. (Multiplying this number by 100 makes it possible to find out the percentage of the flowering stems within one *M. smejkalii* individual). Formula used to calculate the proportion of flowering plants:

$$\textit{proportion of flowering plants} = \textit{flowering stems} / (\textit{non-flowering stems} + \textit{flowering stems})$$



Fig. 5 The measured dimensions on the individual *M. smejkalii* (red circle). Blue arrow (a) maximum length of the tuft, purple arrow (b) show width perpendicular to the length of the tuft. The individuals in the picture are marked with plastic number plates. Photograph Karolína Hrušková 2020

2.3.1.1 Number of flowers per capsule

Important characteristic feature for determining the fitness of plant individual and its effect on population dynamics is the number of flowers flowering on the stems. Flowers on flowering stems were counted in years 2006, 2017, 2018, 2019 and 2020. In contrast to measuring the size of individuals and counting flowering and non-flowering stems, flowers counting on stems was not performed on all *M. smejkalii* individuals. Within each microhabitat, ten flowering individual of *M. smejkalii* were randomly selected.

In these individuals, ten flowering stems were randomly selected and the flowers on them were counted. The flowers were counted only on stems with terminated growth and thus with the maximum number of flowers. Completed growth was defined by dichotomous stem division. This was the reason, why stems with one flower were not included in the count.

In year 2017, it was not possible to select ten random individuals for counting flowers per stems on sites DK1, DK3 and DK4. The reason was the low number of individuals of *M. smejkalii* on the given site or the insufficient number of flowering individuals on the site. In 2018, this problem occurred only at the DK1 site. In 2019 it was not possible to select ten random individuals in the sites DK1 and DK4, and in the last year of measurement (2020), ten flowering individuals were not possible to select at the site DK5. Information on the average number of flowers on the stem was then used (together with number together with the number of seeds in the capsules, see *Chapter 2.3.1.2*) to calculate the average seed production at each site.

2.3.1.2 Seeds per capsule

The capsules were collected also as part of the annual monitoring but only in years from 2017 to 2020. Capsules were collected at all sites. Ten individuals of *M. smejkalii* with already formed capsules were selected by random selection. Five capsules were randomly selected from each selected plant individual. The capsules that were taken had to be mature and unopened (to avoid spilling the seeds before their counting).

The capsules could not be taken in 2017 from the sites DK1 and DK3. The reason was the insufficient number of flowering individuals who formed capsules. In 2018 and 2019, it was not possible to take the capsules at DK1 and DK4. The reason was again an insufficient number of flowering individuals. In the last year of capsule collection (2020), capsules were collected from only three individuals (not five) at the site DK1.

The capsules were then opened under laboratory conditions. Number of seed in the capsule and their appearance were determined. Dark seeds that could be easily separated were determined to be mature. Light brown or yellow seeds, often glued in one difficult-to-divide clump, were identified as immature. Mature seeds were further used for seed bank experiments and to define seed germination (see *Chapter 2.3.1.3* and *2.3.1.4*). The average number of seeds in the capsule was further used to determine the average seed production of *M. smejkalii* individuals in each site.

2.3.1.3 Seed bank

M. smejkalii is a species forming a soil seed bank (Pánková, 2011). Seed survival in the seed bank had to be determined by experiments with burying the collected seeds. During site monitoring two experiments focused on seed survival in a seed bank were performed. The seeds were placed in nylon bags and buried in natural sites approximately 15 cm above the soil surface. The seeds were always buried at the end of the growing season in the first half of September. The first experiment was performed in ten replicates, the second experiment was performed in five replicates.

The first experiment was established in 2007. The experiment contained ten sets. Each set contained three nylon bags. Fifty *M. smejkalii* seeds collected from natural localities were placed in each bag. The first bag from each set was not buried, the seeds from it were sown immediately in 2007 and germinated in laboratory conditions. These immediately sown seeds served as a control for buried bags. In 2009 (after two years), second bags of seeds were excavated, which were germinated immediately after excavation in laboratory conditions. The last (third) bags remained in the soil and were not excavated until 2019 (12 years after the burial). After excavation, these seeds were also sown and germinated in laboratory conditions.

After excavation seeds from one nylon bag were placed in a small petri dish, lined with 3 layers of filter paper, poured with distilled water and placed in a germination box and allowed to germinate. The seeds were in the germination box until they stopped germinating (a month from the time when the last seed germinated). After germination was completed, gibberellic acid was always added to possibly induce growth of the remaining ungerminated seeds. The germination box was set at 12 hours light and 17 ° C and 12 hours dark and 7 ° C. The seeds were watered with distilled water once a week and every second week were germinating seeds counted and the number of germinated and non-germinated seeds was recorded.

The second experiment with buried seeds in bags began in 2017. Five sets of bags were buried. Each set contained five bags. There were thirty *M. smejkalii* seeds in each bag. In 2017, 4 bags from each set were buried. One bag from each set was not buried and the seeds were immediately sown and served as a control for the buried bags.

In 2018, a second bag was excavated from each set and the seeds were germinated in laboratory conditions. In 2019, a third bag was excavated from each set and again the seeds from these bags were germinated in laboratory conditions. Germination was performed under

the same conditions as in the first experiment (see above). Two bags in each set remained in the soil at the sites. Their excavation and analysis are planned in year 2022 (5 years after burying) and in year 2027 (10 years after burying).

2.3.1.4 Sowing experiment

In 2017, seeds were sown directly on exposed substrate in natural sites. At sites DK1, DK2, DK3 and B1 were selected squares measuring 0.5 x 0.5 meters. The squares were marked with nails with colored plastic lids. Half of the squares were sown with seeds at the beginning of the growing season (March) the remaining squares were sown with seeds at the end of the growing season (September). Seeds collected from the previous growing season (2016) were used for spring sowing and were stored in a cool (8 ° C), dark and dry environment until sowing. Fresh seeds from 2017 were used for autumn sowing.

The aim of the experiment was to find out what is the germination of seeds in the field and whether the germination of fresh seeds (from 2017) and seeds from the previous vegetation season (from 2016) differs. The amount of seeds used for sowing at each site is recorded in *Table 3*. The table also shows the number of new individuals that arose on the given sowing areas. Sowing areas are inspected every year as part of ongoing monitoring.

Sowing experiment 2017		
Site	Number of seeds	New individuals
DK1	1944	0
DK2	5320	0
DK3	315	0
B1	1432	13

Table 3 Number of seeds sown at individual sites in 2017 during the sowing experiment. The *New individuals* column shows the success of individual sowings = how many new individuals at the site were created using a sowing experiment.

2.4 Climatic data

Pánková (2011) states that the population dynamics of *M. smejkalii* is influenced by climatic and habitat conditions. The climatic factors that could be used to verify this assumption were monthly sum of precipitation and the average monthly air temperature. Information about total precipitation and temperatures in the years 2006 to 2020 was provided by the Czech Hydrometeorological Institute. Near the monitored localities are located 8 stations of the Czech Hydrometeorological Institute are located (see *Map 4*).

Station Hulice (15.0866 °E, 49.7211 °N – WGS84) was chosen as the wateriest station for providing climate data. At this station, continuous measurement of air temperature and precipitation in the required period (2006-2020) takes place. The station performs measurements at an altitude of 378 meters above sea level, which also corresponds to the altitude of the monitored localities (Hadce u Hrnčír - 426-458 meters above sea level, Hadce u Želivky 385-425 meters above sea level). Other stations did not meet the requirements (inappropriate altitude, later establishment of the station and the beginning of the measurement period, measurement of other climatic parameters and others.)



Map 4 Location of stations of the Czech Hydrometeorological Institute. Red dots with a white centre show the location of monitored sites. The Hulice station was chosen as the most suitable station for the use of climatic data. Map taken from the portal of the Czech Hydrometeorological Institute (https://www.chmi.cz/files/portal/docs/poboc/OS/stanice/ShowStations_CZ.html), edited by K. Hrušková 2020

The influence of climate (temperature and precipitation) was not added to the final IPM. The climate was reflected only in partial models characterizing the most important vital rates in the life cycle of *Minuartia smejkalii*. Mean temperatures and the sum of precipitation between March and June were added to models describing the growth, survival and flowering of *M. smejkalii* (see Table 7).

2.5 Habitat data

At the level of microhabitats was measured the amount of incident light on the site. Hemispherical photographs were used to detect incident light (see *Fig. 6*) (Hardy et al., 2004; Rich, 1990). Data on incident radiation and tree layer canopy were measured in 2007, 2009 (before management interventions) and in 2016-2020 (after management interventions). Information about management interventions can be found in *Chapter 2. 6*. Hemispherical photos were taken by camera with a fisheye (SIGMA 4.5 / 2.8 EX DC CIRCULAR Fisheye HSM Nikon). Data (photos) were processed using Gap Light Analyzer (GLA). The procedure for the analysis of hemispherical photographs performed according to Frazer et al. (1999).

Information about incident radiation per m^2 (radiation units are $mol / m^2 / d$) and about the openness of the tree layer was used from the photographs. The number calculated for the openness of the tree layer characterizes the closedness of the tree crowns (100 = without tree canopy, 0 = maximum tree layer, no light transmission) (Frazer et al., 1999). The incident radiation and openness of the tree layer were not added to the overall IPM. These habitat-specific properties (only from year 2020) were added to selected models characterizing vital rates such as growth, survival and flowering of *M. smejkalii* (see *Table 7*).



Fig. 6 Hemispheric photograph prepared to evaluate the incident radiation on the site in GLA. Photo from year 2016, site DK1, author Hana Pánková

2.6 Management of localities

The first management interventions were carried out at site B1 in 2007. At site B1 was removed the black dump and the area after the old quarry was opened with an excavator. Other

management interventions took place in 2016-2020, especially within the LIFE for *Minuartia* project. Activities such as: felling of trees (pioneer trees and *Picea abies*), removal of vegetation (removal of intensely expanding *Vincetoxicum hirundinaria* species at site DK1), removal of substrate (especially humus layers overlapping serpentine outcrops), mowing of the herbaceous layer (after the vegetation season of *M. smejkalii* and removal of biomass) and as well as fencing of serpentine outcrops with the occurrence of *M. smejkalii* (protection of individuals from animal herbivory). The application of interventions in all localities in the period 2016-2020 is summarized in *Table 4* below.

Management interventions					
Site	2016	2017	2018	2019	2020
DK1	Vegetation removal	Tree felling, Vegetation removal	Tree felling, Vegetation removal		
DK2		Tree felling	Tree felling, Fencing of serpentine outcrops		
DK3	Substrate removal		Tree felling, Substrate removal		
DK4			Tree felling		
DK5			Tree felling		
B1	Opening of the area of the old quarry	Substrate removal	Substrate removal	Tree felling	
B2		Tree felling	Tree felling, Substrate removal		
H	Mowing the grass	Mowing the grass	Mowing the grass, Tree felling	Mowing the grass, Substrate removal	Mowing the grass, Tree felling

Table 4 Overview of all management interventions that took place at the sites with occurrence *Minuartia smejkalii* in the years 2016-2020 within the *Project Life for Minuartia*.

The impact of management interventions was not included in the overall IPM. The effect of felling trees at sites was captured using hemispherical photographs, which capture the incident radiation and the tree layer characteristics. The effect of tree felling at sites has been added to models through the above-mentioned hemispherical photographs. Other management interventions are not included in the models and their possible influence on population dynamics is only discussed in the discussion.

2.7 Data analysis

The data were analysed using the R program version 4.0.2 (R Core Team, 2020). For the analysis of individual categories in the life cycle of *M. smejkalii* were generated fifteen models

(see *Table 6*). Analysis of seven of the fifteen models was performed using the Linear Mixed Effect model (LMER) (Bates et al., 2015). The remaining eight models were analysed using the Generalized Linear Mixed Effect Model (GLMM). The use of LMER and GLMM was conditioned by the need to include random factors (Year, site, square) in the models. GLMMs have been used to analysed subsets with nonnormal distributions (e.g. binomial distributions) (Bolker et al., 2009; Venables and Ripley, 2002). The selection of the best model was made based on the Bayesian information criterion (BIC). BIC is used for larger data sets rather than the Akaike information criterion (AIC) because it is more stringent in the selection of influential predictors in models (Burnham and Anderson, 2002; Kass and Raftery, 1995). The analyses were performed in the R program extended by the *lme4* package (Bates et al., 2015).

2.7.1 Creation of integral projection models

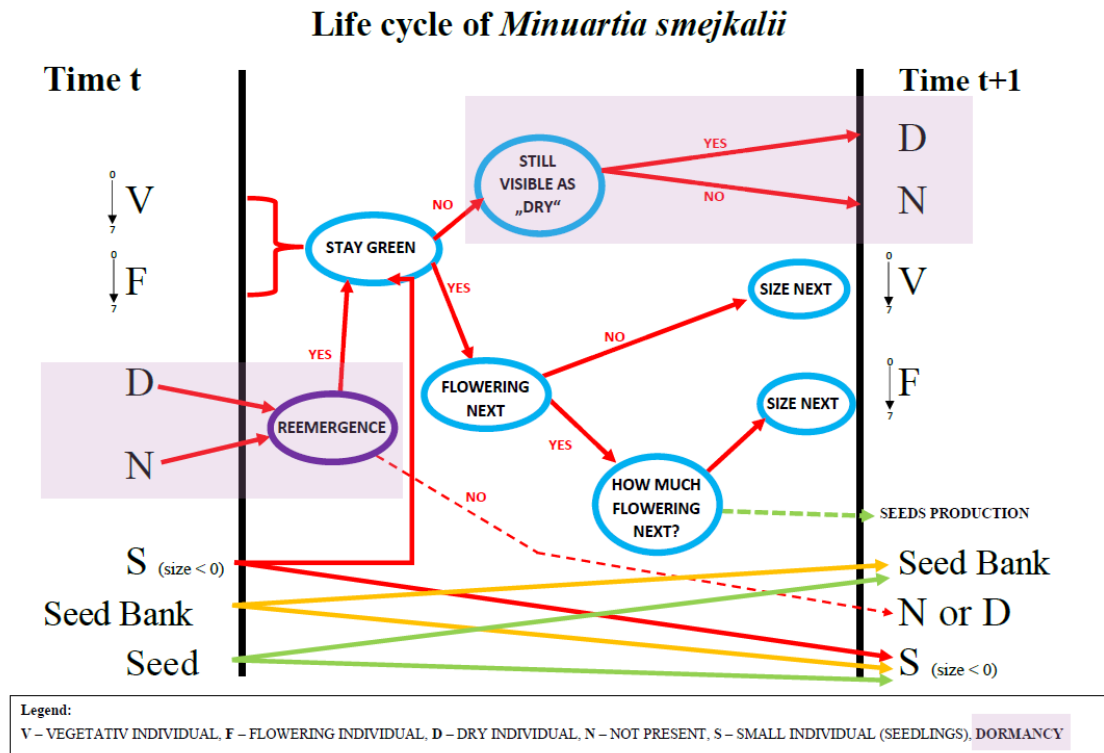
The method Integral projection model (IPM) was chosen as a suitable statistical method for analyses. Commonly used matrix models require the division of a given species into discrete categories (Caswell, 2001). IPM works with continuous variables and helps to understand the influence of an individual on the population dynamics of a species (Rees et al., 2014). At the same time, IPM makes it possible to link climate and data with habitat species dynamics data (Merow et al., 2014).

The construction of the IPM was performed in the R program version 4.0.2 (R Core Team, 2020). The program has been extended with packages: *popdemo* and *fields*. The *popdemo* package was used to work with the IPM mega matrix and to create individual kernels of the final IPM (Stott et al., 2012). The *fields* package was used due to the *image.plot* method which draws an image plot with a legend based on either a regular grid (IPM mega matrix). IPM construction was performed according to Merow et al. (2014) appendix A and Ellner et al. (2016).

3 Results

3.1 Life cycle of *Minuartia smejkalii*

To understand and design the right models characterizing the population dynamics of *M. smejkalii*, it was necessary to describe in detail its life cycle. Schematically, the life cycle is shown in Fig. 7.



The diagram captures the transition of all life stages in *year (t)* to the *year following (t + 1)*. An individual of *M. smejkalii* can go through up to seven categories in its life. In the population there are individuals in the vegetative stage (in the scheme marked V), individuals flowering (marked F), individuals of very small sizes (i.e. 0.5×0.5 cm and 1×1 cm). These small individuals are marked S in the diagram. Then in the diagram are two categories corresponding to individuals forming a dormant stage. Individuals identified in the diagram by the letter D are those who were found dry on the site. *M. smejkalii* often dries after flowering and seed formation. In the following year, these dry plants may remain dry and thus remain dormant. The dry plant may also form green stems or die the following year. The second group, characterized by its possible dormancy, is the plants marked N in the diagram. At the time of monitoring no manifestation of these plants was recorded at the site. These plants may be dormant without above ground expression or they may have died, and we will

not notice them at the site in the next few years. The last two categories shown in the diagram correspond to the seeds and the seed bank. Each stage in the life cycle of *M. smejkalii* and especially the transitions between these categories are captured through IPM.

3.2 Dataset diagnostics and construction of Integral projection models for *M. smejkalii*

The dataset used for the construction of the IPM contained information about all eight populations with the occurrence of *M. smejkalii* in the Czech Republic. See *Table 5*. Only population B2 was excluded due to the insufficient number of individuals in the locality.

Population	Num. of individual	Use in the model
B1	1324	✓
B2	3	✗
DK1	62	✓
DK2	1151	✓
DK3	458	✓
DK4	418	✓
DK5	157	✓
H	1212	✓
Total sum	4785	

Table 5 Table of all populations of *M. smejkalii* with numbers of individuals (records) in given populations from 2006 to 2020. The last column captures whether the data was used for creation of IPM. B1,2 = Bernartice; DK 1, 2, 3, 4, 5 = Dolní Kralovice; H = Hrnčire

The dataset contains information about *M. smejkalii* individuals from 2006 to 2020. This fifteen-year series of measurements was interrupted in 2012, when only the population Hrnčire was measured. Other populations were not measured. In 2013, site monitoring did not take place. Measurements continued from 2014. The year 2013 is therefore completely omitted from the models. In 2012, the sizes of individuals in unmeasured populations were averaged (DK1, DK2, DK3, DK4, DK5). Individuals from unmeasured populations who had sizes in 2011 and 2014 were considered to have existed in 2012, and their size from these two years was averaged.

3.2.1 Selection of suitable models and parameters for IPM

Models were created for each of the seven categories in the life cycle and for all their transitions. The most important step was to choose the right independent variables that the models will contain. Each model contained a dependent variable and was further tested with

five independent variables, which were: *size* and *size per second*, *proportion of flowering*, *proportion of flowering per second* and finally *interactions between size and flowering proportions* of individuals. In addition, all models included random factors *year* of monitoring and *site* with a nested factor of permanent *square*. The random factor *site* with a nested factor of a permanent *square* was important especially for the later application of climatic and habitat factors, which were measured at the level of squares.

The selection of the best model was made based on the smallest Bayesian information criterion (BIC). A list of all created models is in *Table 6*. Models with BIC = 0 were selected as the best. The numbers for the other models show how much worse the model was than the selected model.

In the model describing the return of dry individuals (D) and individuals without visual expression (N) from dormancy two more independent variables were added to the model. The first *DN* variable describing the different probability of returning from dormancy for dry individuals and individuals without visual expression. The second added variable was *YearsSinceGreen*. This variable took into account the number of years when the plant was observed to be dry or without visual expression. The *DN* and *YearsSinceGreen* variables were tested in all models containing dry individuals and individuals without visual expression at the site. However, their significant improvement of the model was reflected only in the model describing the return of D and N individuals from dormancy.

Dependent variable	Independent variable					
	~ size	~ ... + I(size^2)	~ ... + proportionFlowering	~ ... + I(proportionFlowering^2)	~ ... + size:proportionFlowering	
VFgreenNext	4300	4286	0	0	8	... + *
VFfloweringNext	1377	1380	0	5	12	... + *
VFproportionFloweringNext	28	41	0	10	21	... + *
VFsizeNext	0	15	25	34	45	... + *
dryNext	801	808	0	6	7	... + *
DstayD	0	5	-	-	-	... + *
DNreemerge	1041	1048	0	6	4	... + DN + YearsSinceGreen + *
DNsizeAfterDormancy	0	9	-	-	-	... + *
DNflowerAfterDorm	0	3	-	-	-	... + *
VFclonalPropagation	134	143	0	6	12	... + *
ClonalOffspringSizeNext	94	99	6	4	0	... + *
ClonalOffspringFloweringNext	38	41	3	6	0	... + *
FseedProduction	10043	10057	218	37	0	... + *
DNproportionFloweringAfterDorm	0	9	-	-	-	... + *
VFsizeAfterDorm	0	9	-	-	-	... + *

* (1 | site / square) + (1 | year)

Table 6 List of all models and tested independent variables. Selected models with the best BIC are highlighted in green. All models included a random factor of year and a site with nested factor of permanent monitoring square.

The models were the basis for parameterizing the IPM mega matrix. In total fifteen models defining fifty-six parameters (estimates for each independent variable) were created. For some of the rarer transitions between categories in the life cycle have been created constants. The reason for the creation of constants was the small number of observed cases in the life cycle of *M. smejkalii* (for example the clonal formation of individuals by the disintegration of the tuft) or the calculation of the probabilities of transition based on experiment with the seed bank. In total thirty constants describing the categories of seedlings, seed bank and the formation of individuals by the disintegration of tufts (clonality) were created. According to the models were created eighty-six parameters forming the IPM mega matrix.

3.2.2 Number of individuals of *M. smejkalii* between years 2005-2020

The first attention in the study was paid to the development of the numbers of individuals of *M. smejkalii* over the monitored years 2006-2020 in all localities (without the missing year 2013). This development of the numbers of individuals shows *Fig. 9*.

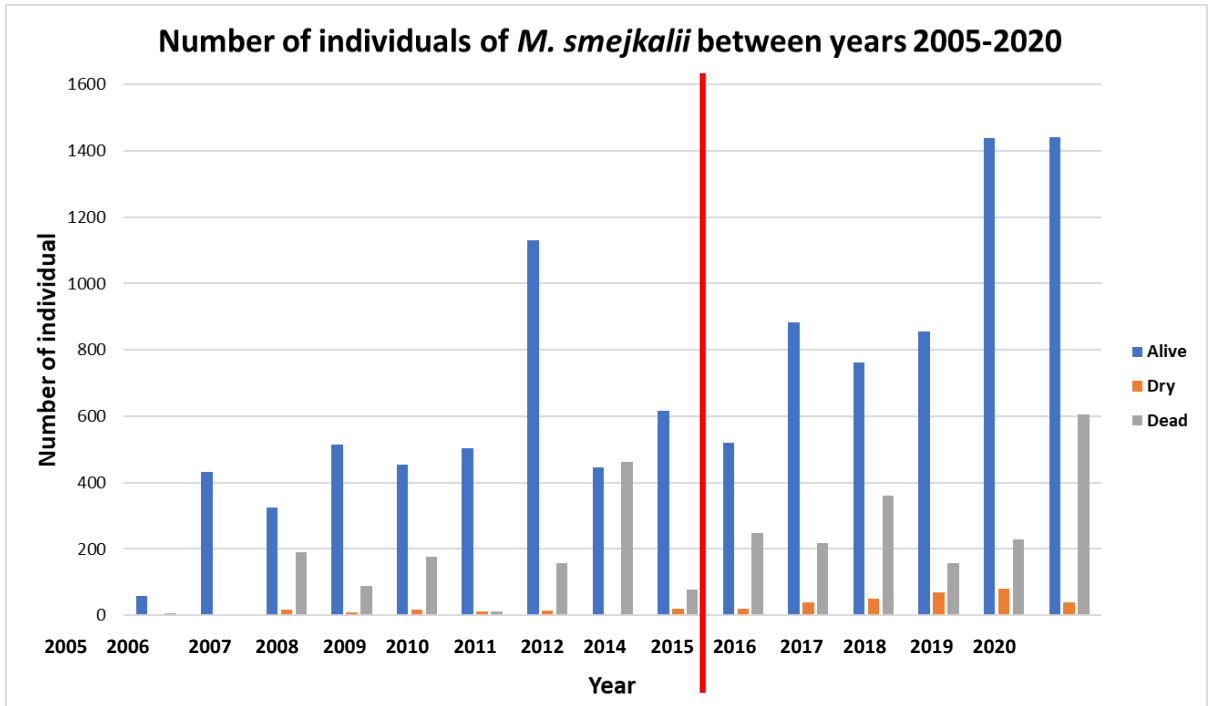


Fig. 8 The figure shows the development of the numbers of all individuals of the species *Minuartia smejkalii* in the years 2005-2020. The numbers of vegetative and flowering individuals at the localities are recorded in blue columns, the individuals found at the localities in the dry state are shown in orange columns. Dead individuals of the species are shown in grey columns. The red line shows the beginning of site management since 2016.

During the years 2006-2015, it is possible to observe the state of the *M. smejkalii* population in the range from 400 to 600 individuals across all populations. An exception is the year 2011, when there was an increase in the number of individuals and a subsequent increase in mortality in 2012, which responded to a high number of new individuals in 2011. An increase in the number of individuals in 2011 and their high mortality in 2012 was observed at localities Hrnčíře (H). High mortality at the Dolní Kralovice 2 (DK2) site is a possible relic of missing data due to the absence of monitoring in year 2012 on this site. The data in year 2012 were averaged for the DK2 site from year 2011 and 2014 just for vegetative and flowering individuals which were active in 2011 and also 2014. Therefore, data on the exact mortality of *M. smejkalii* individuals from year 2012 at all habitats (except for Hadce u Hrnčíř) are inaccurate.

Since 2016, a gradual increase in the number of new individuals can be observed. In 2020, the number of monitored individuals at localities were more than 1400. Overall, the higher number of individuals corresponds to their increased mortality, but mortality does not reach such values as in 2012. The increase in individuals since 2016 is affected probably by the beginning of management measures. Namely, it involves the felling of overgrown trees, the removal of substrate layer and mowing of grasslands. More detailed information on the course of management interventions is given in more detail in the *Chapter 2. 6*

3.2.3 The size of *M. smejkalii* individuals

The size of individuals *M. smejkalii* was calculated as the area of the ellipse (see *Chapter 2.3.1*). Using the diagnosis of the occurrence of sizes within the whole population, it was found that the variable size is significantly negatively skewed and does not correspond to the normal distribution (see *Fig. 10*). After transforming the data using the natural logarithm, this skew was removed, and the data approached the normal distribution. (see *Fig. 11*).

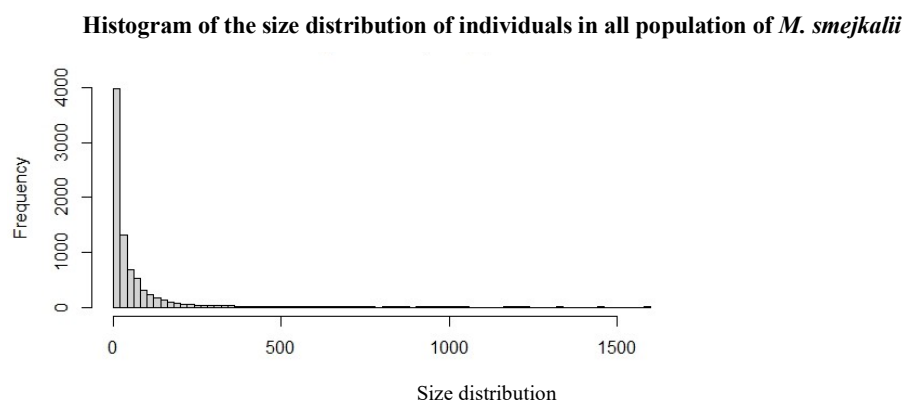


Fig. 9 Histogram of the size distribution of individuals in all population of *M. smejkalii*

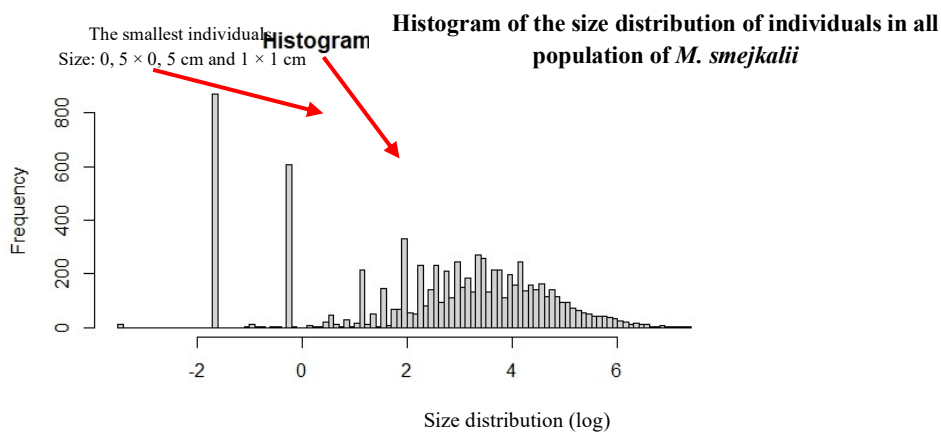


Fig. 10 Histogram of distribution of transformed size by natural logarithm in all population of *M. smejkalii*.

In *Fig. 11*, even after the transformation, two large columns of values remained in the range -1.627 and -0.241. These columns represent the smallest individuals, seedlings with sizes of 0.5×0.5 cm and 1×1 cm. These smallest individuals in the *M. smejkalii* population were evaluated separately within the IPM, as their behaviour differed from the rest of the population (for example, a high increase in the number of individuals and their subsequent high mortality). The variable *size* of the rest of the population of *M. smejkalii* was treated as a continuous variable.

3.2.3.1 Relationship between the size of *M. smejkalii* individuals in year t and in year $t + 1$

Another question related to the size of individuals is whether individuals increase, decrease, or remain the same size in the transition from year (t) to the following year ($t + 1$). The analysis of the subset (flowering and vegetative individuals) was performed using linear mixed effects models (LMER). The selection of the best model based on BIC is shown in *Table 6*, row VFsizeNext.

The size of individuals *M. smejkalii* in year $t + 1$ is significantly influenced by the size of individuals in year t . Individuals of small size up to the size of $\log 4$ grow more than the average predicted by the model. Individuals larger than $\log 4$ grow less than the model's average growth. The relationship between the size of the plant in year t and the following year is shown in *Fig. 12* below. The proportion of flowering in year t has no effect on the size of the plant in year $t + 1$.

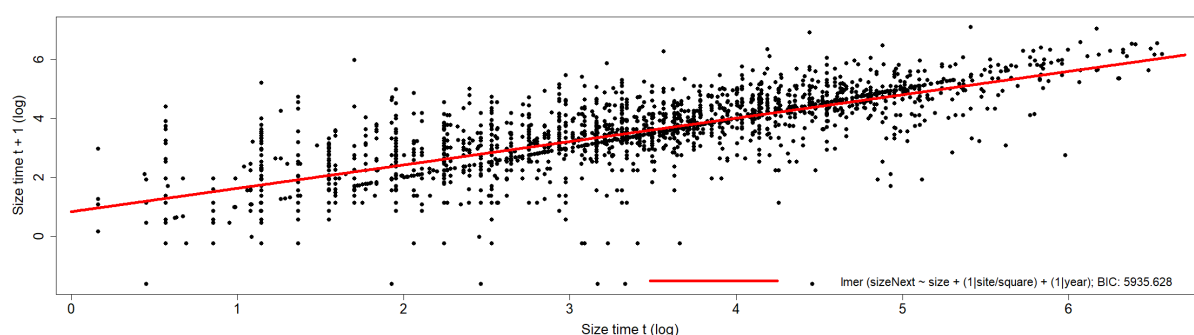


Fig. 11 Influence of the size of *M. smejkalii* individuals in year t on size in year $t + 1$.

3.2.4 Vegetative and flowering individuals in the life cycle of *Minuartia smejkalii*

In connection with flowering and vegetative individuals it was necessary to answer several questions. The first two questions were: What will affect the activity of the plant next year? How likely is that the individual will become vegetative or flowering again?

The analysis of the subset (flowering and vegetative individuals) was performed using generalized linear mixed-effects model (GLMM) with a binomial distribution (plant stays green until next year or not). The most suitable model selected based on the BIC is shown in *Table 6*, row VFgreenNext.

The size of an individual in year t has a significant influence on whether *M. smejkalii* will be active (i.e. green - vegetative or flowering) in the following year $t + 1$. The influence of the size of individuals in year t on their activity in year $t + 1$ is shown in *Fig. 13*. The probability that an individual will be active again in year $t + 1$ increases with its size in year t .

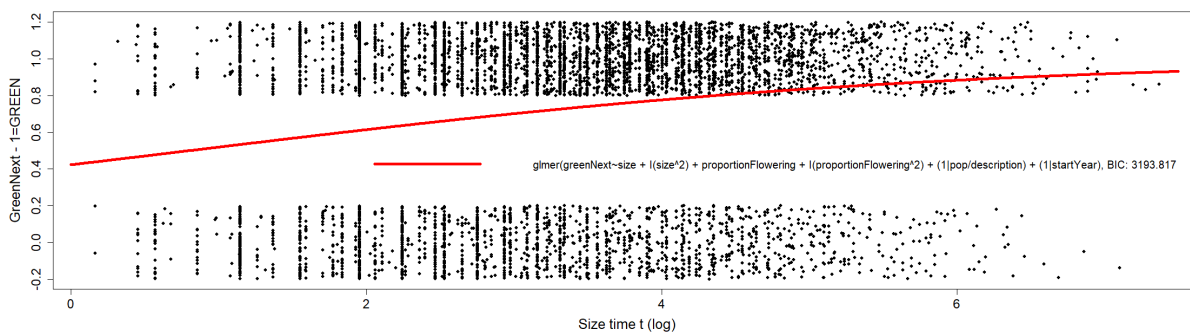


Fig. 12 Influence of the size of *M. smejkalii* individuals in year t on their activity in the year $t + 1$. The x-axis shows the size of the individual in year t (log). The y-axis shows the activity of individuals: 1 = the individual is active (vegetative or flowering) in year $t + 1$, 0 = the individual is dry or without visual expression

The second predictor influencing the activity of *M. smejkalii* individuals in the following year was the proportion of flowering. The probability that *M. smejkalii* will be active even in year $t + 1$ significantly decreases with the proportion of flowering in year t . If a larger percentage of stems of an individual are flowering, the likelihood that the individual will be active next year decreases. The decrease is also evident in the graph of the model in *Fig. 14*.

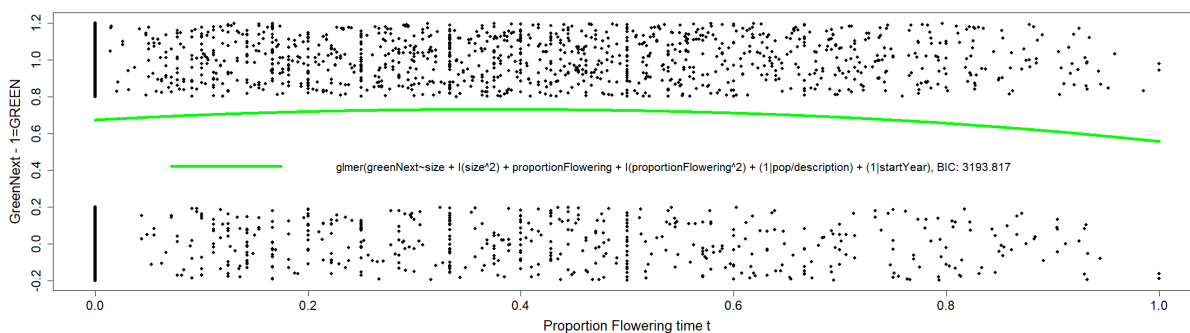


Fig. 13 Influence of porportion of flowering in year t on the activity of *M. smejkali* individuals in year $t + 1$. The x-axis shows the proportion of flowering at time t . The y-axis shows the activity of individuals: 1 = the individual is active (vegetative or flowering) in year $t + 1$, 0 = the individual is dry or without visual expression

3.2.4.1 Probability of flowering and proportion of flowering in the next year $t+1$

Other questions associated with vegetative and flowering individuals in the life cycle of *M. smejkalii* were: If the individual is active, what will affect flowering? And if an individual blooms, what will affect how much the individual blooms?

To answer the first question of whether an individual will bloom in the following year analysis of a subset of flowering and vegetative individuals was performed using GLMM with binomial distribution (flower or not). The selection of the best model based on BIC is shown in *Table 6*, row VFfloweringNext.

The probability that an individual will bloom in the following year is significantly affected by the size of the individual in year t . The probability that an individual will bloom in year $t + 1$ increases with the size of the individual in year t . This dependence is shown in *Fig. 15*.

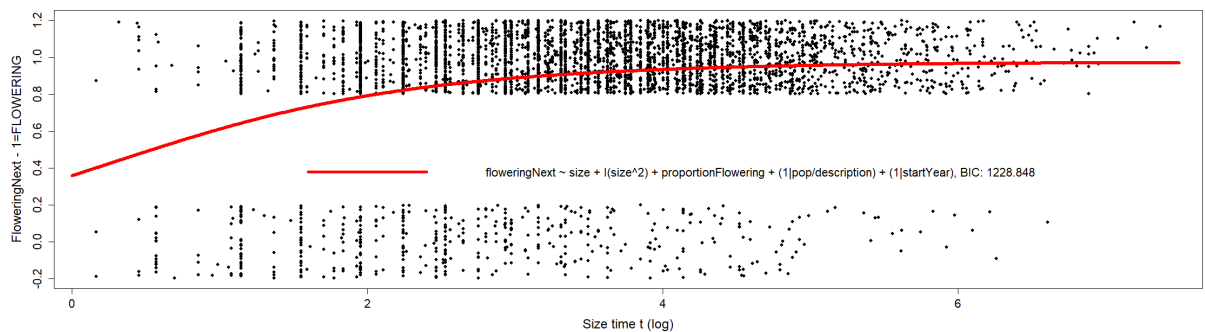


Fig. 14 Influence of individual size in year t on flowering of individual in year $t + 1$. The x-axis shows the size of the individual on a logarithmic scale. The y-axis shows flowering individuals ($y = 1$) and vegetative individuals ($y = 0$)

Another factor that significantly affects whether the individual of *M. smejkalii* will bloom in the following year is the proportion of flowering in year t . The probability that the individual will bloom in year $t + 1$ increases with the proportion of flowering in year t . This dependence is shown in *Fig. 16*. An individual with most flowering stems will be more likely to flower the following year than an individual with most non-flowering stems.

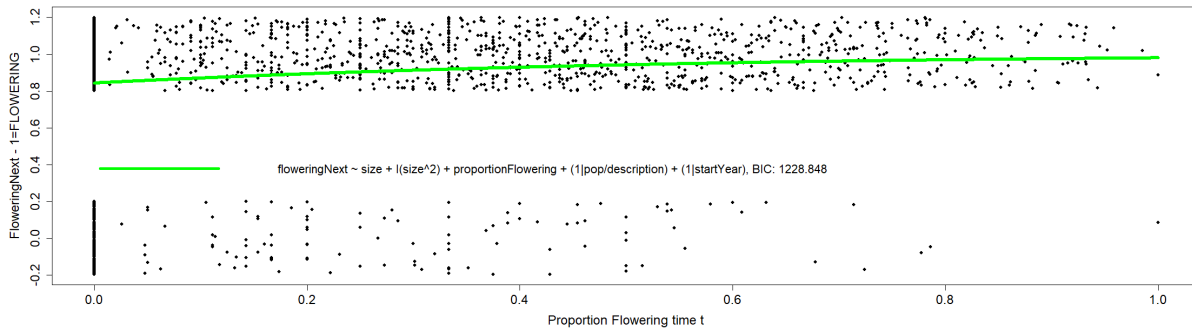


Fig. 15 Influence of flowering proportion in year t on probability of flowering in year $t + 1$. The x-axis shows the proportion of flowering in year t , the y-axis shows flowering individuals ($y = 1$) and vegetative individuals ($y = 0$) in year $t + 1$

To answer the second question (what affects the proportion of flowering) subset of vegetative and flowering individuals was analyzed using LMER. The selection of the best model based on the BIC is shown in *Table 6*, row VFproportionFloweringNext.

The size of individuals in year t influences the proportion of flowering in year $t + 1$. Medium-sized individuals of *M. smejkalii* have on average more flowering stems than individuals of small and largest sizes. The dependence is evident in *Fig. 17*.

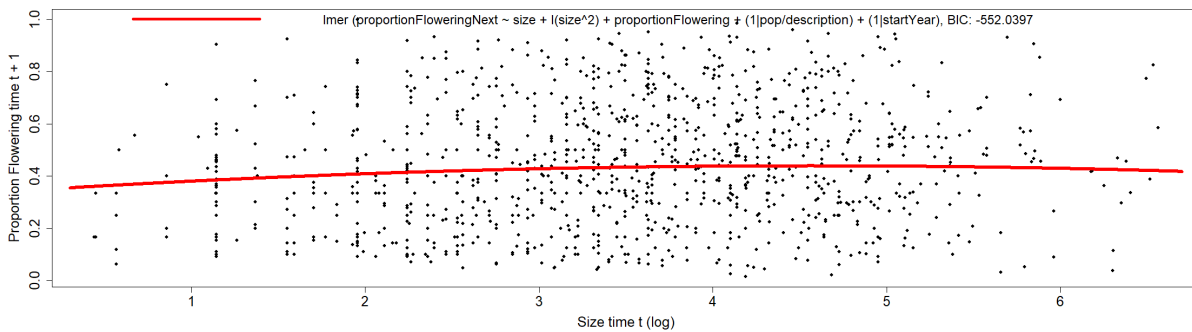


Fig. 16 Influence of the size of *M. smejkalii* individuals in year t on the proportion of flowering in year $t + 1$. The x-axis shows the size of individuals in year t on a logarithmic scale. The y-axis expresses the proportion of flowering in year $t + 1$. $y = 1$ - all stems on an individual are flowering, $y = 0$ - no stems on an individual are flowering

The proportion of flowering in year $t + 1$ is also affected by the proportion of flowering in year t . With the increasing proportion of flowering in year t , the proportion of flowering in year $t + 1$ also increases. The dependence is shown in *Fig. 18*. The influence of the proportion of flowering in year t on proportion of flowering in year $t + 1$ is mainly influenced by individuals who do not form any flowering stems in year t and have relatively high flowering proportions in year $t + 1$. (see *Fig. 18*, x-axis = 0 and a wide range of values for the y-axis)

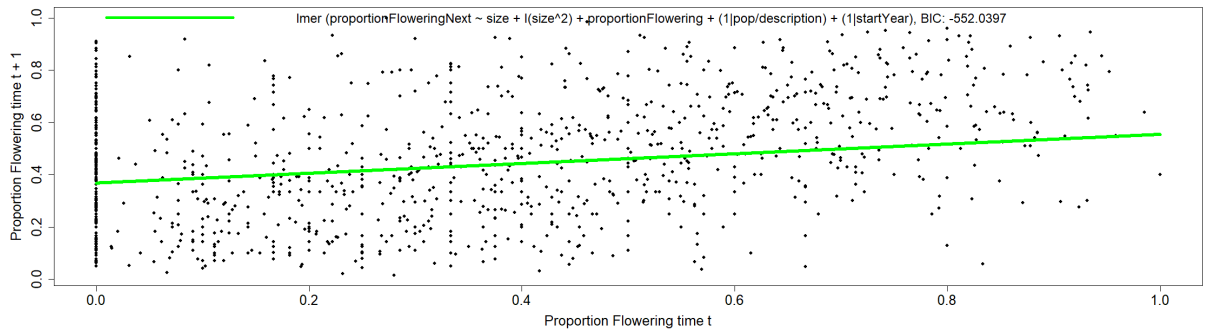


Fig. 17 Influence of the proportion of flowering in year t on the proportion of flowering in year $t + 1$. The x-axis shows the proportion of flowering of individuals in year t . The y-axis expresses the proportion of flowering in year $t + 1$. $x, y = 1$ - all stems on an individual are flowering, $x, y = 0$ - no stems on an individual are flowering

3.2.5 Dry plants in the life cycle of *Minuartia smejkalii*

In the life cycle of *M. smejkalii* are individuals who were recorded as dry plants during monitoring. These dry plants were in a dormant state and were able to reactivate after a few years. Such re-activation was detected in 235 individuals of *M. smejkalii* during the monitoring period 2006-2020.

First, it was necessary to determine whether the size or proportion of flowering of an individual in year t will affect its condition in year $t + 1$ (dry or individual without visible expression). The analysis was performed on subset of individuals which were recorded as vegetative or flowering in year t and recorded as dry individual or individual without visible expression in year $t + 1$. The analysis was performed using GLMM with binomial distribution (dry or individual without visible expression). The selection of the best model based on BIC is shown in *Table 6*, row *dryNext*. The result of the model is that the size and proportions of flowering has a significant influence on whether the plant in year $t + 1$ will be dry (D) or without visual expression (N). With increasing size and proportion of flowering increases the probability that the individual in year $t + 1$ will be D rather than N. Large flowering individuals are more likely to occur as D than N.

The second question associated with dry individuals was: What is the chance that the dry plant will remain dry until the next year? Will any relationship be affected by any independent variable? To answer this question, a model analysing a subset of individuals D (i.e. dry) in year t on becoming dry or individual without visible expression in year $t + 1$ was used. The analysis was performed using GLMM with binomial distribution (i.e. dry or individual without visible expression). The selection of the best model based on BIC is shown in *Table 6*, row *DstayD*.

The model showed a significant effect of the size before the dry state on the probability that the individual will go to state D (dry) rather than to state N (without visual expression). This dependence is shown in *Fig. 19*. Larger individuals of *M. smejkalii* remained in a dry state for a longer time (3 and more years) than they were active again. Most dry individuals (73%) return to the active state after 1 year in the dry state. After two years in the dry state 17% of individuals return to the active state, after 3 years 6% and after 4 or more years only 4% of dry individuals return to the active state.

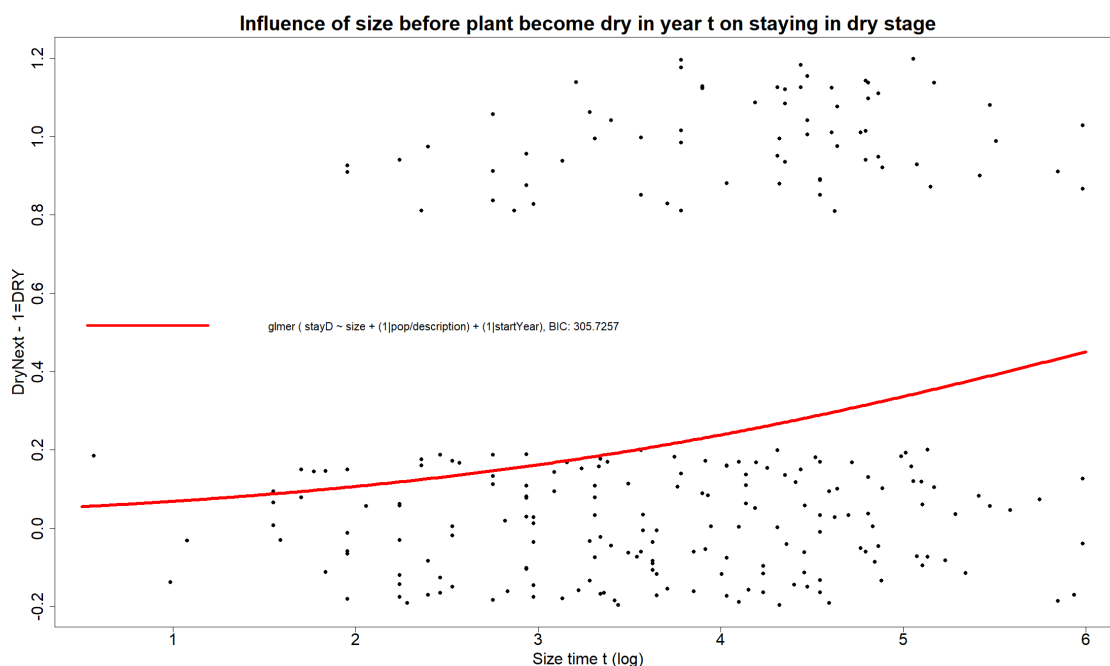


Fig. 18 Influence of individual size in year t on its condition in year $t + 1$. The x-axis shows the size on a logarithmic scale, the y-axis shows the status of individuals in the year $t + 1$. $y = 1$ - individuals dry (D) in year $t + 1$, $y = 0$ - individuals without visible expression (N) in year $t + 1$. Larger individuals will be more likely to be in state D than N in year $t + 1$ than N.

3.2.6 Dormant individuals in the life cycle of *Minuartia smejkalii*

Minuartia smejkalii is able to endure in a dormant state. Dormant individuals of *M. smejkalii* are either in a dry state persistent on serpentine outcrops or are not visible and survive in the crevices of serpentine outcrops or in the soil. Understanding the functioning of this part of the life cycle of *M. smejkalii* is difficult. It is demanding to determine whether the individual is in a dormant state or the individual has died.

The first question about dormancy: What influences the return of individuals *M. smejkalii* from dormancy? To answer this question, a subset of individuals D and N who returned from a dormant state to an active state (vegetative or flowering) was analysed. Subset analysis was performed using GLMM with binomial distribution (stay dormant or become

green). The selection of the best model based on BIC is shown in *Table 6*, row DNreemerge. During this analysis, two independent variables were added to the model, namely *DN* and *YearsSinceGreen*. Both variables significantly improved the BIC of the model.

The return of *M. smejkalii* individuals from dormancy is affected by the size of the individuals before entering the dormant state, the duration of the dormant state (*YearsSinceGreen*) and the manifestation of the dormant state - whether the individual is D or N (*DN*). The probability of returning from dormancy increases with size in year t . A larger individual is more likely to return from a dormant state to an active state. Furthermore, the probability of an individual returning from dormancy decreases with the length of time in dormancy and the manifestation of a dormant state. Individuals who are in state N are less likely to return from dormancy than individuals in state D.

Survival of dormant plants was set at five years. Only one individual was able to activate after 7 years in a dormant state. Individuals who were found to be dry (D) had a 17% probability of being active again after one year in dormancy. In contrast, individuals who were dormant without visual expression (N) had only a 5% chance of being active again after one year in dormancy. If the individual is dry, it is easier for it to return from dormancy to the active state.

The second question associated with dormant individuals was whether the size in year t before entering dormancy would affect the size of the individual after returning from dormancy? To answer this question, an analysis was performed of individuals who were in state D or N in year t and were active (vegetative or flowering) in year $t + 1$. The analysis was performed using an LMER. The selection of the best model based on the BIC is shown in *Table 6*, rows DNsizeAfterDormancy and VFsizeAfterDorm. The result of the model was that the size of *M. smejkalii* individuals after dormancy was not affected by the size of the individuals before entering dormancy.

The last two questions associated with dormant individuals dealt with the issue of flowering individuals after returning from dormancy. Third question: Does the size in year t (before entering dormancy) affect whether the plant will bloom after returning from dormancy? To answer this question an analysis of subset of individuals who were in state D or N in year t and were active (vegetative or flowering) in year $t + 1$ was performed. The analysis was performed using an GLMM with binomial distribution (flower or not). The selection of the best model based on the BIC is shown in *Table 6*, row DNflowerAfterDorm. The result of the model

was that the size of *M. smejkalii* individuals before entering dormancy does not affect the probability of flowering after the return of individuals from dormancy.

The last fourth question is also related to flowering: If an individual blooms after it returns dormancy, will the size of the year before entering dormancy affect the proportion of flowering? To answer this question an analysis of subset of individuals who were in state D or N in year t and were flowering in year $t + 1$. The analysis was performed using LMER. The selection of the best model based on the BIC is shown in *Table 6*, row DNproportionFloweringAfterDorm. The result of the model was that the size of *M. smejkalii* individuals before entering dormancy does not affect the proportion of flowering after the return of individuals from dormancy.

3.2.7 Clonal propagation by the disintegration of tufts of *Minuartia smejkalii*

As part of the monitoring of the population dynamics of *M. smejkalii*, the disintegration of tufts of some individuals was also monitored. Disintegration of one individual's tuft created one or more new daughter's individuals. Between 2006 and 2020 forty-seven new individuals of *M. smejkalii* were formed by clonal propagation.

The first question associated with this phenomenon was what influences the emergence of a new daughter's individuals? To answer this question, a model analysing a subset of individuals V and F (i.e. vegetative and flowering) in year t was used. The analysis was performed using GLMM with binomial distribution (i.e. individuals producing clones and individuals without clonal propagation). The selection of the best model based on BIC is shown in *Table 6*, row VFclonalPropagation.

The result of the model was that the size and proportion of flowering of the mother plant in year t influences the formation of new daughter's plant. With the increasing size and proportion of flowering of the mother plant the probability of the formation of a daughter's plant increased. New daughter individuals were formed most often by medium-sized and medium-flowering mother plants.

Another question was whether the characteristics of the mother plant would affect the size and proportion of flowering of the daughter plant? The effect of the size and proportion of flowering of the mother plant on the size of the daughter's plant was tested first. To answer this question, a model analysing a subset of daughter was used. The analysis was performed using

LMMER. The selection of the best model based on BIC is shown in *Table 6*, row ClonalOffspringSizeNext.

The result of the model was that the size and proportions of the mother plant in the year before the disintegration of the mother tuft influence the size of the daughters. With the increasing size of the mother plant, the size of the daughters increased. However, with increasing proportion of flowering of the mother plant, the size of the daughters decreases. This model also showed a significant positive effect of the interaction of the size and proportion of flowering of mother plants on size of daughters. The inclusion of interaction in the model has significantly improved its BIC.

The second tested was the effect of the size and proportion of flowering of the mother plant on the proportion of flowering of the daughter's individual. To answer this question, a model analysing a subset of daughter individual was used. The analysis was performed using GLMM with binomial distribution (i.e. vegetative of flowering). The selection of the best model based on BIC is shown in *Table 5*, row ClonalOffspringFloweringNext.

The result of the model was that the size and proportion of flowering of the mother plant in the year before the disintegration of the mother tuft influenced the proportion of flowering of the daughters. With the increasing size of the mother plant, the proportion of flowering of the daughters increased. However, with increasing proportion of flowering of the mother plant, the proportion of flowering of the daughters decrease. This model also showed a significant positive effect of the interaction of the size and proportion of flowering of mother plants on daughters. The inclusion of interaction in the model has significantly improved its BIC.

3.2.8 Seedlings and their fate in the life cycle of *Minuartia smejkalii*

Minuartia smejkalii seedlings are individuals defined by their age. Individuals who did not form clonally from year t to year $t + 1$ or did not return from dormancy were defined as new individuals - seedlings. Seedlings are able to bloom and produce seeds in the first year of their life. More than half of the monitored seedlings larger than 1×1 cm bloomed in the first year. Smaller seedlings up to 1×1 cm bloomed in only 1.3% of cases. On average, 1.2 seeds were produced per seedling per year. Larger seedlings had a larger proportion of flowering. On average, the larger seedling has 35% of flowering stems in the tuft. The probability that the seedling will be dry next year is 0.8%, that it will become a non-flowering individual is 14%, the probability of developing a flowering individual from seedling is 17% and the probability that the seedling will be without visual expression (i.e. dormant or dead) is 67.3%.

The probability that the seedling will return from a dormant state to an active one is only 3%. Recovery from dormancy was recorded only after one year. Longer-time dormant seedlings were not reported. After returning from dormancy in 75% of cases the seedlings become medium-sized flowering individuals.

3.2.9 Seed production in the life cycle of *Minuartia smejkalii*

The seed production of *M. smejkalii* is crucial for the life cycle and the formation of the seed bank. The average number of seeds produced per individual is 1864 seeds per year. Seed production in the *M. smejkalii* population does not have a normal distribution. To bring the seed production closer to the normal distribution, the data were transformed using the natural logarithm. This removed the positive skewness of the data. The aim of the data analysis was to determine whether the size and proportions of flowering affect seed production. The analysis was performed using LMER. The selection of the best model based on BIC is shown in *Table 6*, row FseedProduction.

The result of the model was that the size and proportion of flowering influences seed production. The seed production of an individual increases with its size and proportion of flowering. The effect of individual size on seed production is shown in *Fig. 20* and the effect of flowering proportion on seed production is shown in *Fig. 21*. The model also showed a positive interaction between size and flowering proportions. The interaction significantly improved the BIC of the model. Individuals of *M. smejkalii* reaching large sizes with a large proportion of flowering produce many seeds. The highest calculated production of one individual was 64 400 seeds per plant per year.

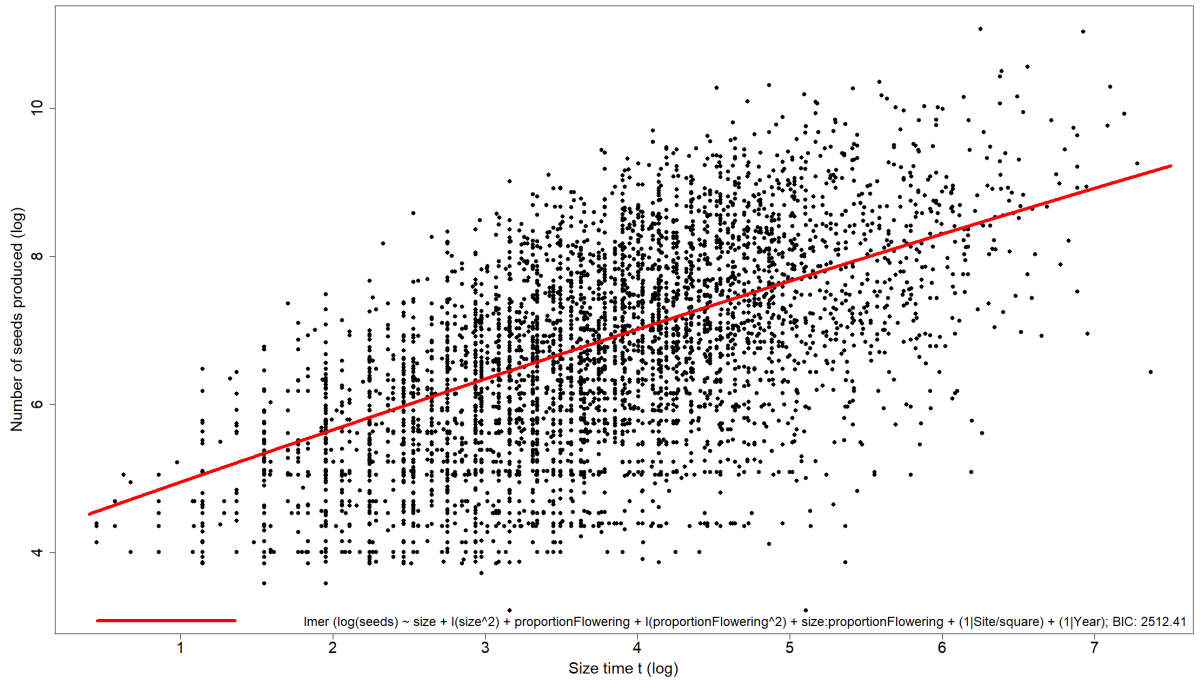


Fig. 19 Influence of the size of *M. smejkalii* individuals on seed production. The x-axis shows the size of individuals in year *t* on a logarithmic scale, the y-axis shows seed production on a logarithmic scale.

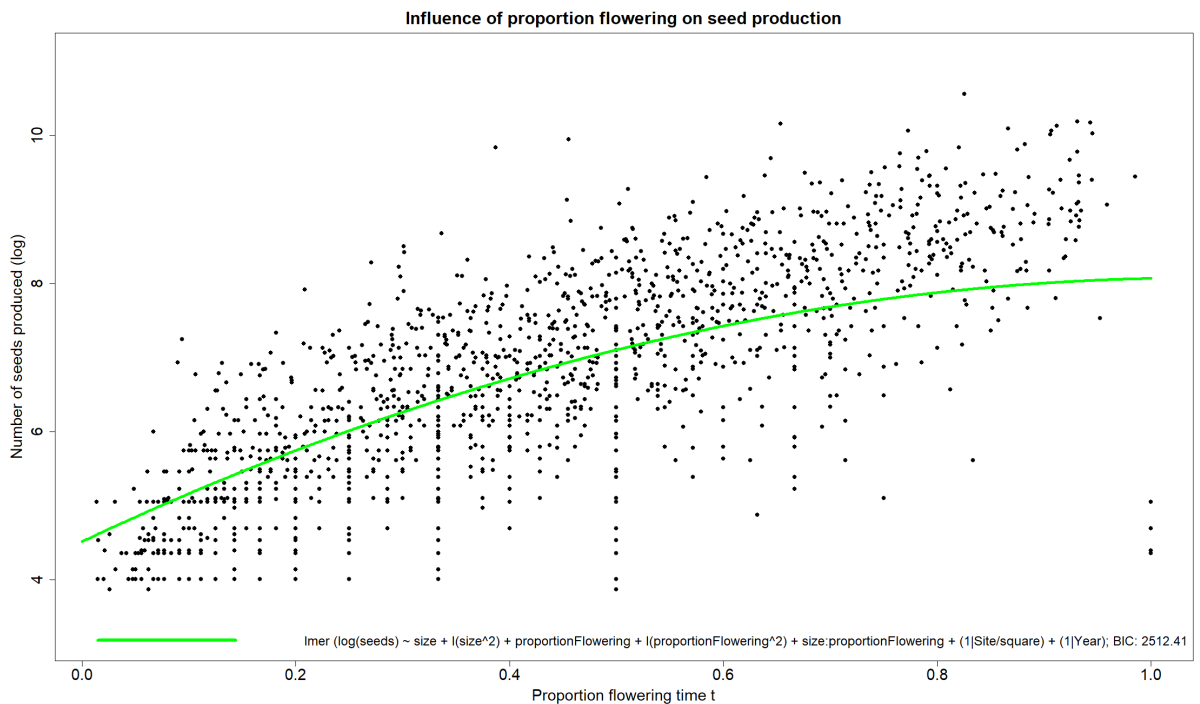


Fig. 20 Influence of the proportion of flowering of *M. smejkalii* individuals on seed production. The x-axis shows the proportion of flowering of individuals in year *t* on a logarithmic scale, the y-axis shows seed production on a logarithmic scale.

3.2.10 Seed bank

Using an experiment with buried nylon nags with seeds (see *Chapter 2.3.1.3*) it was possible to determine the survival of *M. smejkalii* seeds in a seed bank. Buried seeds

(representing seeds from a natural seed bank) are able to germinate even after 10 years in the soil. Therefore, the viability of the seeds in the seed bank was set to 10 years. The average annual decrease in seed germination in the seed bank was set at 14.7%.

Unfortunately, the sowing experiments (see *Chapter 2.3.1.4*) failed. Seed germination occurred only on one sowing square at site B1. Sowing success was very low, only 0.9%. The site B1 was hit by heavy rains in the year of sowing experiment and the material was flooded. The probability of contamination of seeds from the natural population in the sown square is quite high. Therefore, the results of the sowing experiment were not included in the modelling of the population dynamics of the species.

Based on the results of an experiment with buried bags and knowledge of seed production and the emergence of seedlings in natural localities, it was possible to calculate the transitions of seed in the life cycle of *M. smejkalii* from year t to year $t + 1$. The probability of survival of the seed in the seed bank (from year t to $t+1$) is 85.3%. Furthermore, the probability that one individual will produce a new individual in the following year is 0.007%. The percentage of produced seeds that enter the seed bank is 99%. Finally, the probability that a new individual is from a seed bank is 0.01%. These very low probabilities of formation of new individual are partially compensated by probably large seed production (see *Chapter 3.2.9*).

3.3 Influence of climatic and habitat conditions

After constructing models describing all transitions in the life cycle of *M. smejkalii*, it was possible to add the influence of climate and habitat to these models. Climatic data were used from the climatic station of the Czech Hydrometeorological Institute. More information about climatic data in *Chapter 2.4*. The Hulice station recorded the daily average air temperature and total daily precipitation. The period of the first half of the vegetation season, i.e. March to June, was chosen as a suitable climatic window influencing the population dynamics of *M. smejkalii*. The use of climatic factors from the selected period March to June is stated as appropriate in Adler (2012). According to Adler (2012), the average spring temperature before the beginning and at the beginning of the growing season has the greatest influence on the transitions between growing seasons. The effect of the sum of daily precipitation during the growing season is presented as influential in Torang (2010); Dalglish (2011) and Nicole (2011).

Based on the above studies daily precipitation for a given period of each year were summed up. Summed precipitation entered the vital rates models. Temperatures for the selected

period from March to June were averaged and this value entered the vital rate models. Habitat conditions were represented by radiation and the canopy openness of the tree layer at each site. Habitat data were used only from the year 2020. The reason was the smallest percentage of missing data.

Before adding climate to the IPM, five models describing basic vital rates (survival, growth and flowering) were selected. Selected models and the climatic and habitat factors added to these models are listed in *Table 7* below. The “blank” model is the best model (based on the best BIC) from *Table 6*.

BIC							
Dependent variable	blank model	... * Temperature	... * Precipitation	... * Temperature * Precipitation	... * Radiation	... * Canopy	Vital rates
VFgreenNext	0	15	15	45	10	6	survival
FseedProduction	0	17	37	80	81	31	survival
VFsizeNext	0	4796	4777	4858	4781	4784	growth
VFflowerNext	0	11	13	33	12	9	flowering
VFproportionFloweringNext	0	26	42	103	26	29	flowering

Table 7 List of models characterizing vital rates *M. smejkalii*. Models are distinguished based on BIC. BIC = 0 - best model, models with other numbers describe how much worse the given models are than the best model. *VFgreenNext* and *FseedProduction* are models describing the survival of *M. smejkalii* individuals (green color). *VFsizeNext* is a model describing the growth of individuals (red color) and *VFflowerNext* and *VFproportionFloweringNext* are models describing the flowering of *M. smejkalii* individuals.

All selected models describing vital rates were tested with the addition of climatic and habitats factors. Subsequently the BICs of models with added climatic and habitat factors were compared with the BIC of the blank model. The addition of climate influence and habitat factors to models describing vital rates did not result in a significant improvement in the BICs of those models.

Based on these results, climatic and habitat factors were not incorporated into the final IPM. Their insertion into the IPM will be appropriate later. Prerequisite for the correct addition

of climatic and habitat factors to the IPM is the discovery of the correct climatic window, which affects the population dynamics of *M. smejkalii*.

3.3.1 Evaluation of population dynamics of *Minuartia smejkalii* using IPM

Based on models describing the life cycle of *M. smejkalii* 86 parameters using the above-described models were defined. For details about parameters see *Chapter 3.2.1*. These parameters helped to parameterize the final IPM mega matrix. The mega matrix contains 202x202 cells. The first 10 cells of x axis in the IPM mega matrix are ten size categories of vegetative plants. Another 80 cells are ten size categories of flowering individuals divided into eight categories according to the proportion of flowering. Next 100 cells are five categories of dry individuals and individuals without visual expression. Each of these categories (D, N) again contains ten size classes. The following are two categories of seedlings. The last 10 categories in the IPM mega matrix are ten years of seed banks. The order of the life cycle categories of *M. smejkalii* in the IPM mega matrix and their elasticity is summarized in *Fig. 22*.

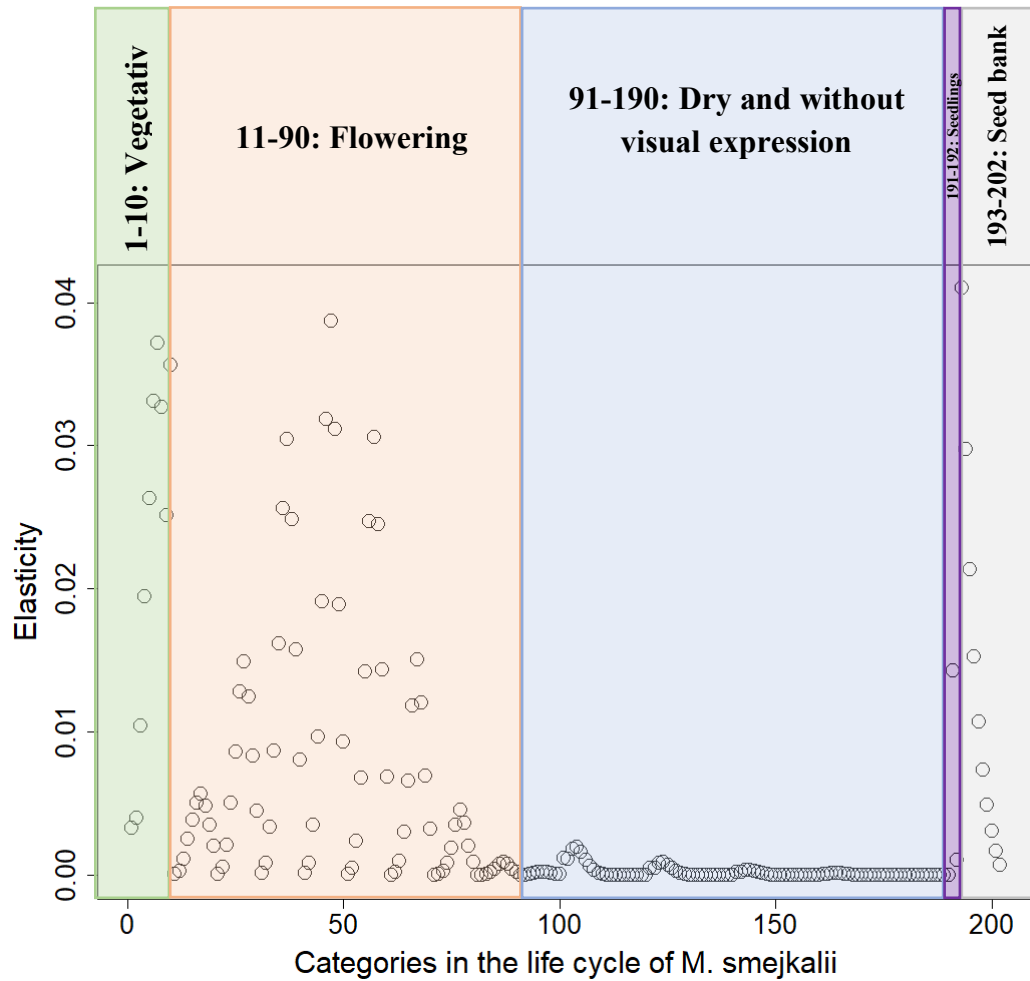


Fig. 21 Elasticity of categories in the life cycle of *M. smejkalii* and their order in the IPM mega matrix. The x-axis contains categories in the life cycle: 1-10 cells of vegetative individuals (green square), 11-90 cells of flowering individuals (red square), 91-190 cells of dry individuals and individuals without visual expression (blue square), 191-192 cells of seedlings (purple square), 193-202 cells of seed bank (gray square). The y-axis shows the elasticity of the categories.

The first IPM was made up of three kernels, namely clonal propagation (Cmat), survival (Pmat) and sexual production (Fmat). Based on the elasticities of the individual matrix kernels, it was found that the largest proportional change in population growth is caused by Pmat (79%). The second most influential kernel was Cmat with an elasticity of 16%. The last Fmat kernel had an elasticity only 5%. The population growth rate (λ) was calculated at 1.155 based on the model. The first IPM and the contributions of the individual kernels are shown in Fig. 23, 24. Figure 23 and 24 were rescaled ($\cdot 0.1$)

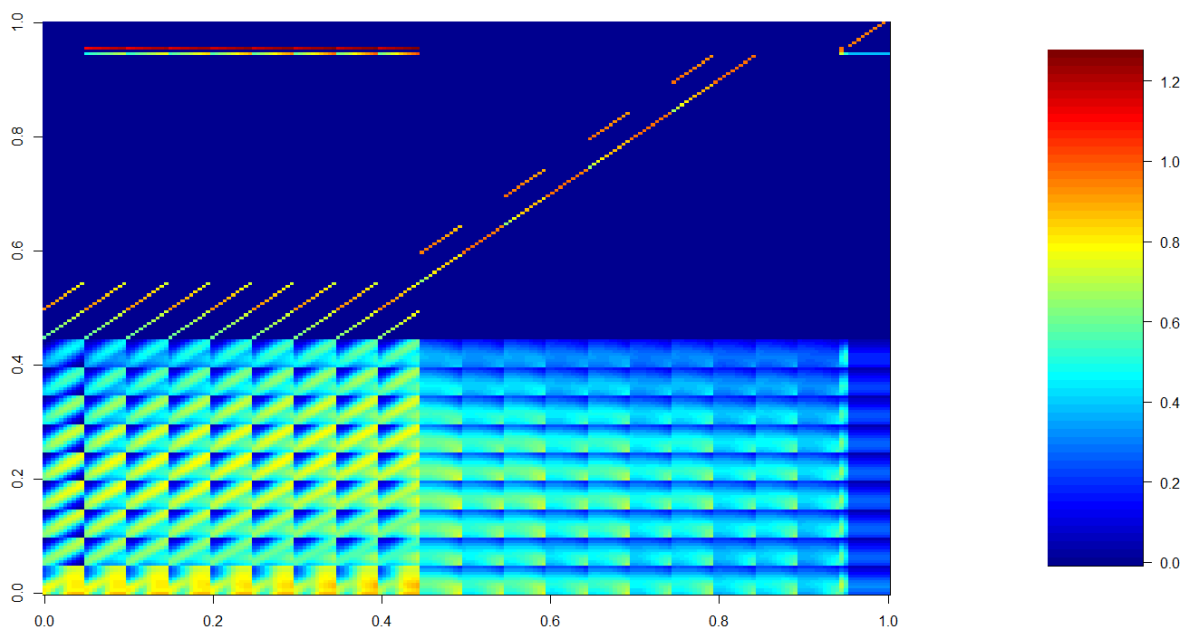


Fig. 22 The first IPM composed of three kernels. Rescaled by 0.1. Categories on both axes correspond to Fig. 22.

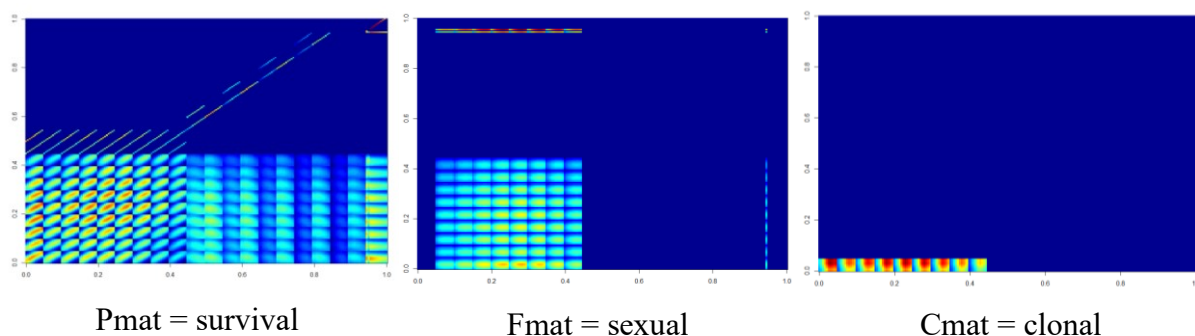


Fig. 23 Contribution of individual kernels to population growth. Rescaled by 0.1

In the case of the first IPM was made significant contribution of Cmat (clonal propagation) to the change in population growth. The formation of clonal individuals does not occur as often in natural populations, and therefore another IPM without Cmat was created. The second IPM consisted of only two kernels, Fmat and Pmat. In this case, the elasticity of Pmat reached 79% and the elasticity of Fmat 21%. The population growth rate (λ) was lower than in the previous model, namely 1.014. The second IPM and the contributions of the individual kernels are shown in Figs. 25, 26. Figures 25 and 26 were scaled with 0.1.

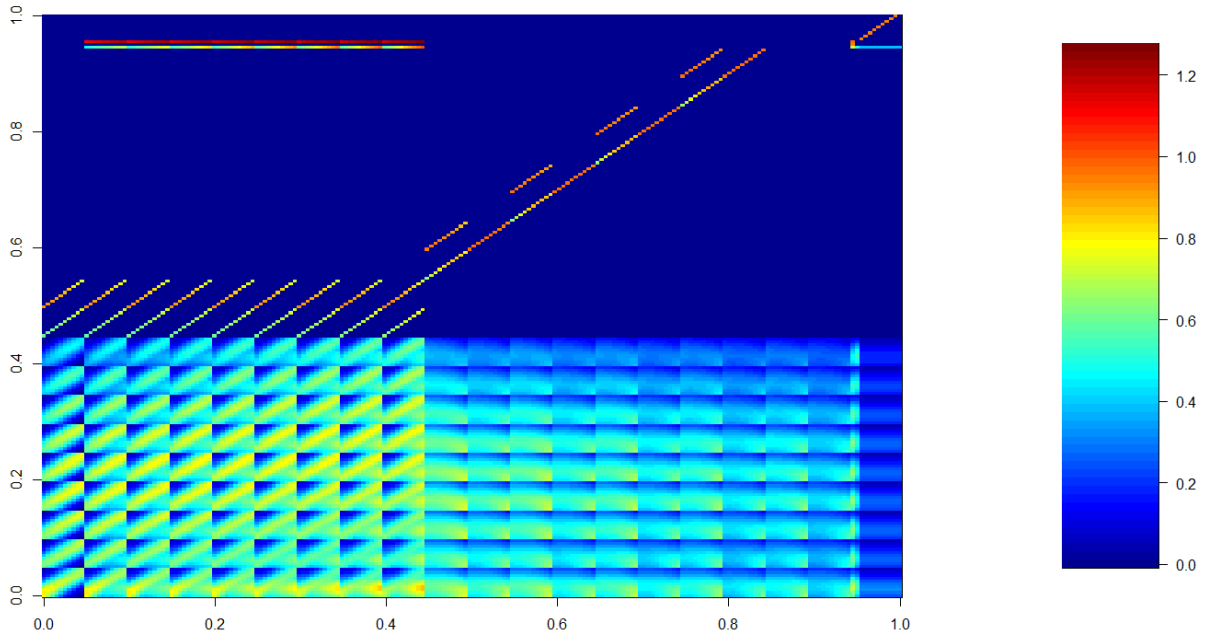


Fig. 24 IPM model without clonality, so composed only of survival and reproduction. Rescaled by 0.1. Categories on both axes correspond to Fig. 22.

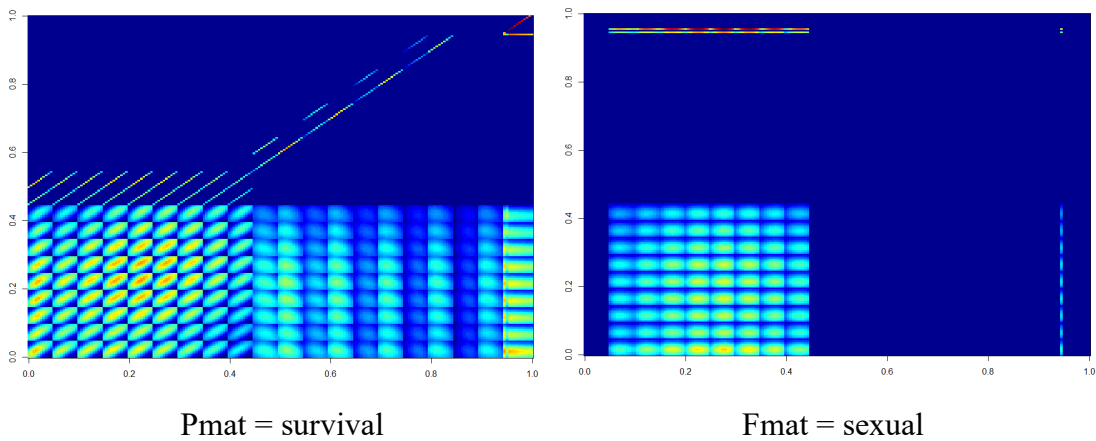


Fig. 25 Contribution of individual kernels to population growth in the IPM model without clonality. Rescaled by 0.1. Categories on both axes correspond to Fig. 22.

Based on the elasticity of individual kernels, the survival of *M. smejkalii* individuals has the main influence on population dynamics. The first model also showed a very significant effect of clonality. Later, it will be appropriate to add the influence of climate and habitat conditions to the models and monitor the influence of these factors on the population growth rate of *M. smejkalii*.

4 Discussion

4.1 Missing data in the dataset

Each field dataset contains missing values (Nakagawa, 2011). Within the population modelling of the species *M. smejkalii* it is necessary to deal with the missing values for the year 2013 and for some sites in the year 2012. How to deal with this problem depend on the parameter to which the missing values relate. In the dataset two approaches are used to solve this problem. The data were either averaged using a weighted average between years 2011 and 2014 or omitted from modelling the population dynamics of the species. In the dataset were averaged the missing *size* values for living individuals in the year 2012 at all sites at the locality Hadce u Želivky. Individuals who lived in both years (2011 and 2014) were declared alive in 2012. The *seed production* was also averaged for these individuals in the same way as *size*. The year 2013 cannot be averaged retrospectively. This year would create inaccuracies in modelling population dynamics and therefore the year 2013 was omitted from statistical analyses. Therefore, transition between 2012-2014 was not created. This transition would not be realistic. Averaged data were not used in the model and have only informative value. Delete the cases with missing data is the most common way to deal with problem of missing data in datasets (Nakagawa, 2011). Averaging the values may cause a reduction in the variance of the predictors or may lead to the formation of a bias parameter (Freckleton, 2011).

4.2 Seed production, germination and seed bank

Although *M. smejkalii* produces many seeds (on average 1800 seeds per individual per year), the establishment of new seedlings from fresh seeds is very low (only 0.007%). In contrast the probability that a new seedling will arise from seed from a seed bank is 0.01%. It is therefore possible that the better germination of the seeds is influenced by their persistence in the seed bank. Factor that significantly influences the germination and survival of seeds in the seed bank is the climate (Ooi, 2012). Very little is currently known about the effect of climatic conditions on the seed bank (Thompson, 2000). Seed dormancy in most plant species is induced by substrate temperature. On the other hand, activation of germination is conditioned by precipitation (Baskin et al., 1998). High air and substrate temperatures can cause seed germination failure or seed latency (Lloret et al, 2004). On the other hand, many plants survive unfavourable temperature extremes by seeds in the seed bank (Fenner and Thompson, 2005).

The influence of the climate on the seed bank of *M. smejkalii* can be considered in the year 2011 when there was a multiple increase in the number of new individuals at the locality Hadce

u Hrnčář. The increase in the number of individuals is recorded in *Fig. 9*. Therefore, it is necessary to model the survival of seeds in the seed bank and the transitions between the seed, the seed bank and the seedling as accurately as possible. Currently, the influence of seed banks has been inserted into the model as a constant. Due to the lack of data, it was not possible to determine the exact annual contribution of the seed bank. The seed bank's contribution may vary from year to year. For example, based on the influence of climatic conditions. Modelling the annual influence of the seed bank could improve the IPM model of *M. smejkalii*.

4.3 Sowing experiment

Sowing experiment is a common approach to determine seedling recruitment in population models (Münzbergová, 2005). The sowing experiment carried out on the sites to determine the germination of the seeds failed. Its failure was probably greatly influenced by the low germination of fresh seeds (0.007%) and probably poorly chosen sowing areas.

In total, 9009 seeds were sown during the sowing experiment. However, the success rate of new seedling was very low. New individuals were formed at only one site. Unfortunately, the results from this one successful sowing area cannot be included in the experiment. Probably due to intensive precipitation and poor choice of sowing site was the sowing area contaminated with seeds from a natural population located nearby.

Another factor that caused the experiment fail was the low number of sown seeds. With the production of 1 800 seeds per individual, without the influence of the seed bank and with a very low success rate of seedling establishment, 1 seedling is produced per 11 000 produced seeds. In the case of the sites with seed bank, approximately 850 seeds are required to produce 1 seedling. From this relationship, it is clear that the sowing experiment was significantly underestimated in terms of the number of sown seeds.

4.4 Influence of climatic and habitat conditions on vital rates

Population dynamics of *M. smejkalii* is influenced by climatic and habitat conditions (Pánková, 2011). To verify this assumption, the influence of climatic and habitat factors was added to the vital rates models (See *Table 7*). However, none of the models confirmed the influence of climatic and habitat factors on vital rates. To determine the effect of climate, it is necessary to choose a suitable time window when the climate affects vital rates (Evers et al.,

2021). Defining the right environmental factors and determining the exact time window when these factors act is very difficult. Especially in cases where individual environmental factors are correlated with each other (Salguero-Gomez et al., 2015).

What is the best time window and which climatic factors should be included in the analysis? In the literature, the choice of climatic factors and the appropriate time window vary considerably. Most studies test the influence of climatic factors of a given year on the vital rates of a given year. A minority of studies is revealing the effect of climatic factors from year $t-1$ on vital rates in year t (Evers et al., 2021). Influence of climatic factors on vital rates was demonstrated only in cases including only extremes of the given year. For example, extreme temperature and precipitation anomalies. These anomalies that can greatly affect plant vegetation processes (Easterling et al., 2000). In the case of *Minuartia smejkalii*, it would be appropriate to consider the effect of anomalous dry years. To derive this climatic factor, it is possible to calculate the so-called drought index for each year of the monitoring period and include this index in the models characterizing vital rates (Gouveia et al., 2017)

In the case of *M. smejkalii*, it will be necessary to define the correct time window and climatic factors influencing vital rates. It is important to select factors that are not correlated with each other and will not cause causal relationships between other factors and time windows (Evers et al., 2021). After defining the correct time window and climatic and habitat factors influencing vital rates, it will be possible to add these factors to the already prepared IPM.

4.5 Result of integral projection models

In this thesis I created two IPM models. The difference between the models was in the number of kernels making up the IPM mega matrix. The first model contained three kernels. The most surprising was the effect of clonal propagation (Cmat). Although *M. smejkalii* tufts do not disintegrate too often (only 47 cases observed), the resulting individuals have a large effect (16%) on population growth.

A newly formed individual (seedling) from a seed or seed bank is a small plant with low seed production and low probability (only 31%) of survival into the next year. However, by the disintegration of the mother plant tuft is created a large individual with a higher seed production than in the case of a seedling. Clonally produced individuals also have a higher chance of survival until the following year than seedlings. Therefore, these individuals play such an important role in the population growth of *M. smejkalii*. The population growth rate (λ)

of the first model is equal to 1.155, i.e. the population of *M. smejkalii* has a weak population growth.

The second model contained only two kernels, survival (Pmat) and sexual reproduction (Fmat). After removing the clonality effect, the population growth rate decreased to 1.014. This value indicates stable population growth. A comparison of these two IPM models shows that clonal propagation influences the population growth rate of *M. smejkalii*. Other categories in the life cycle that significantly contribute to the effect on population growth rate are seeds deposited in the seed bank, seed survival in the seed bank and survival and reproduction of medium-sized and flowering individuals of *M. smejkalii*.

5 Conclusion

In my work I focused on the population dynamics of the Czech endemic *Minuartia smejkalii*. It is an obligate serpentinophyte species from the family Caryophyllaceae occurring only in two localities, namely Hadce u Želivky National Natural Monument and Hadce u Hrnčír Natural Monument. From 2006 to 2020, population, habitat and climate data were collected. Based on population data, the life cycle of *M. smejkalii* was created. Furthermore, population data were processed using the Integral projected model. Based on the IPM, the population growth rate of the species was determined.

Minuartia smejkalii is a species forming 7 categories in its life cycle, namely: flowering, vegetative, dry individuals and individuals without visual expression, seeds, seed bank and seedlings. Individuals in the dry state and without visual expression form a dormant stage. An individual can remain in the dormant stage for up to 5 years. Survival of seeds in the seed bank is up to 10 years. The transitions between the stages in the life cycle are often influenced by the *size* and *proportion of flowering* of a given individual in the previous year. Individuals of *M. smejkalii* can also be created by clonality. The clonal individual is formed by the disintegration of the mother plant tuft. The number of observed individuals at the localities in the year 2020 was more than 1400.

The population dynamics of *Minuartia smejkalii* is most influenced by seed formation, their transition to the seed bank and survival in the seed bank. Another influential category are medium-sized flowering individuals. Clonal propagation also influences population growth rate. The population growth rate is between 1.014 and 1.155. That is, the population growth rate of *Minuartia smejkalii* is stable or slightly increasing.

Climatic and habitat factors were included only in the models characterizing vital rates. After the addition of climatic and habitat factors, there was no improvement in the models and their significant influence on the vital rates. Therefore, climatic and habitat factors were not further included in the IPM analysis.

Management interventions taking place in the localities are likely to affect the population dynamics of *M. smejkalii* and help to stabilize the serpentine habitat. The effectiveness and impact of management measures need to be further evaluated.

6 References

- Adler PB, Dalgleish HJ, Ellner SP. 2012.** Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology*, **100**: 478-487.
- Anacker BL. 2014.** The nature of serpentine endemism. *American Journal of Botany*, **101**: 219-224.
- Anacker BL, Whittall JB, Goldberg EE, Harrison SP. 2011.** Origins and consequences of serpentine endemism in the California flora. *Evolution*, **65**: 365-376.
- Baskin JM, Nan XY, Baskin CC. 1998.** A comparative study of seed dormancy and germination in an annual and a perennial species of *Senna* (Fabaceae). *Seed Science Research*, **8**: 501-512.
- Bates D, Machler M, Bolker BM, Walker SC. 2015.** Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**: 1-48.
- Bilz M, Kell SP, Maxted N, Lansdown RV. 2011.** *European Red List of Vascular Plants*. United Kingdom: Luxembourg: Publications Office of the European Union.
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS. 2009.** Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, **24**: 127-135.
- Brady KU, Kruckeberg AR, Bradshaw HD. 2005.** Evolutionary ecology of plant adaptation to serpentine soils. *Annual Review of Ecology Evolution and Systematics*. Palo Alto: Annual Reviews.
- Burnham KP, Anderson DR. 2002.** *Model selection and multimodel inference, A practical information-theoretic approach*: Springer-Verlag. .
- Caswell H. 2001.** *Matrix population models*. Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers.
- Chytrý M, Douda J, Roleček J, Sádlo J, Boublík K, Hédli R, Vítková M, Zelený D, Navrátilová J, Neuhäuslová Z, Petřík P, Kolbek J, Lososová Z, Šumberová K, Hrivnák R, Michalcová D, Žáková K, Danihelka J, Tichý L, Zouhar V, Hájek O, Kočí M. 2013.** *Vegetace České republiky*. Praha: Nakladatelství Academia.
- Chytrý M, Kučera T, Kočí M, Grulich V, Lustyk P. 2010.** *Katalog biotopů České republiky*. Praha: Agentura ochrany přírody a krajiny ČR.
- Dalgleish HJ, Koons DN, Hooten MB, Moffet CA, Adler PB. 2011.** Climate influences the demography of three dominant sagebrush steppe plants. *Ecology*, **92**: 75-85.

- Damschen EI, Harrison S, Ackerly DD, Fernandez-Going BM, Anacker BL. 2012.** Endemic plant communities on special soils: early victims or hardy survivors of climate change? *Journal of Ecology*, **100**: 1122-1130.
- Dvořáková M. 1988.** *Minuartia smejkalii*, ein neue Art aus des *Minuartia gerardii*-Gruppe (*Caryophyllaceae*). *Preslia* 60. Praha.
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000.** Climate extremes: Observations, modeling, and impacts. *Science*, **289**: 2068-2074.
- Ellner SP, Childs DZ, Rees M. 2016.** Data-driven Modelling of Structures Population, A practical guide to the Integral Projection Model. Switzerland: Springer international publishing.
- Evers SM, Knight TM, Inouye DW, Miller TEX, Salguero-Gomez R, Iler AM, Compagnoni A. 2021.** Lagged and dormant season climate better predict plant vital rates than climate during the growing season. *Global Change Biology*: 15.
- Fenner M, Thompson K. 2005.** *The ecology of seeds*. United Kingdom: Cambridge university press.
- Frazer GW, Canham CD, Lertzman KP. 1999.** Gap Light Analyzer (GLA): Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. <http://www.rem.sfu.ca/forestry/index.htm>
- Freckleton RP. 2011.** Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error. *Behavioral Ecology and Sociobiology*, **65**: 91-101.
- Gouveia CM, Trigo RM, Begueria S, Vicente-Serrano SM. 2017.** Drought impacts on vegetation activity in the Mediterranean region: An assessment using remote sensing data and multi-scale drought indicators. *Global and Planetary Change*, **151**: 15-27.
- Grulich V, Chobot K. 2017.** Červený seznam ohrožených druhů České republiky. *Příroda, číslo 35*. Praha: Agentura ochrany přírody a krajiny ČR.
- Hardy JP, Melloh R, Koenig G, Marks D, Winstral A, Pomeroy JW, Link T. 2004.** Solar radiation transmission through conifer canopies. *Agricultural and Forest Meteorology*, **126**: 257-270.
- Harrison S, Davies KF, Safford HD, Viers JH. 2006.** Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora. *Journal of Ecology*, **94**: 110-117.
- Hejný S, Slavík B. 1990.** *Květena České republiky 2*. Praha: Academia.

- Kass RE, Raftery AE. 1995.** Bayes factors. *Journal of the American Statistical Association*, **90**: 773-795.
- Lloret F, Penuelas J, Estiarte M. 2004.** Experimental evidence of reduced diversity of seedlings due to climate modification in a Mediterranean-type community. *Global Change Biology*, **10**: 248-258.
- Merow C, Dahlgren JP, Metcalf CJE, Childs DZ, Evans MEK, Jongejans E, Record S, Rees M, Salguero-Gomez R, McMahon SM. 2014.** Advancing population ecology with integral projection models: a practical guide. *Methods in Ecology and Evolution*, **5**: 99-110.
- Munzbergova Z. 2005.** Determinants of species rarity: Population growth rates of species sharing the same habitat. *American Journal of Botany*, **92**: 1987-1994.
- Nakagawa S, Freckleton RP. 2011.** Model averaging, missing data and multiple imputation: a case study for behavioural ecology. *Behavioral Ecology and Sociobiology*, **65**: 103-116.
- Nicole F, Dahlgren JP, Vivat A, Till-Bottraud I, Ehrlen J. 2011.** Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology*, **99**: 1211-1218.
- Ooi MKJ. 2012.** Seed bank persistence and climate change. *Seed Science Research*, **22**: S53-S60.
- Pešout P. 2001.** Final report: the rescue of Dolnokralovice serpentines and part of Vltava slopes in cooperation with owners. *ČSOP, Vlašim*.
- Pánková H. 2011.** *Kuřička Hadcová. Minuartia smejkalii. Péče o druh a jeho lokality*. Praha: Agentura ochrany přírody a krajiny ČR.
- Rees M, Childs DZ, Ellner SP. 2014.** Building integral projection models: a user's guide. *Journal of Animal Ecology*, **83**: 528-545.
- Rich P. 1990.** Characterizing Plant Canopies With Hemispherical Photographs. *Remote Sensing Reviews*, **5**: 13-29.
- Salguero-Gomez R, Jones OR, Archer CR, Buckley YM, Che-Castaldo J, Caswell H, Hodgson D, Scheuerlein A, Conde DA, Brinks E, de Buhr H, Farack C, Gottschalk F, Hartmann A, Henning A, Hoppe G, Roemer G, Runge J, Ruoff T, Wille J, Zeh S, Davison R, Vieregg D, Baudisch A, Altwegg R, Colchero F, Dong M, de Kroon H, Lebreton JD, Metcalf CJE, Neel MM, Parker IM, Takada T, Valverde T, Velez-Espino LA, Wardle GM, Franco M, Vaupel JW. 2015.** The COMPADRE Plant Matrix Database: an open online repository for plant demography. *Journal of Ecology*, **103**: 202-218.

- Stojanova B, Surinova M, Zeisek V, Munzbergova Z, Pankova H. 2020.** Low genetic differentiation despite high fragmentation in the endemic serpentinophyte *Minuartia smejkalii* (*M. verna* agg., Caryophyllaceae) revealed by RADSeq SNP markers. *Conservation Genetics*, **21**: 187-198.
- Stott I, Hodgson DJ, Townley S. 2012.** popdemo: an R package for population demography using projection matrix analysis. *Methods in Ecology and Evolution*, **3**: 797-802.
- R Core Team 2020.** R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Thompson K. 2000.** The functional ecology of soil seed banks. *Seeds: The Ecology of Regeneration in Plant Communities*. New York: CABI Publishing.
- Torang P, Ehrlen J, Agren J. 2010.** Linking environmental and demographic data to predict future population viability of a perennial herb. *Oecologia*, **163**: 99-109.
- Venables WN, Dichmont CM. 2004.** GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. *Fisheries Research*, **70**: 319-337.