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Summary of the Doctoral Thesis

Determinants of orchid species diversity

Determinanty druhové diverzity orchidejí

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ABSTRACT

Natural environment has been significantly altered by human activity in past few decades. There is an evidence that we are now facing the sixth mass extinction and suitable areas for species are getting smaller. Therefore, many species of plants and animals are experiencing strong population decline and some of them even became extinct. We focused our attention on orchids because their distribution expresses one of the highest declines among all plant families.

In this thesis, we investigated species richness and distribution patterns of orchids, the rate and causes of their decrease and extinction, and factors influencing their occurrence in the Czech Republic and Greece. In the majority of the presented papers, we used a dataset based on the database of the Nature Conservation Agency of the Czech Republic that includes more than 115 000 of orchid records in the country. We also analysed the patterns in the six different phytogeographical regions in the Czech Republic that differ in altitude and the composition of local flora. The key findings are as follows:

- The specialized pollination strategy of orchids, as well as type of rooting systems, both in the Czech Republic and in Greece, play a role in the distribution patterns of orchids in the two countries (Papers I, II and VI). Moreover, the trends differed between the six floristic regions (Paper I and II). In the Czech Republic, the most widely distributed orchid group are the rhizomatous orchids, whereas tuberous orchids were the most widely distributed orchids in Greece (Paper I and VI). We assume that these differences in the trends might be based on the orography of the country, distribution of suitable habitats and types of bedrock.
- The highest decline in orchid distribution during the time periods studied was recorded for critically endangered taxa (Paper III). The number of suitable sites for the Czech orchids declined by 8–92%, depending on the species (Paper IV). One of the most threatened orchid species is *Spiranthes spiralis*. The distribution of orchids in the Czech Republic is mainly affected by the distribution of their habitats.
- The most important factor affecting the distribution of Czech orchids in the region of South Bohemia was the land cover, expressed as the consolidated layer of ecosystems (KVES). The other two important environmental predictors were the mean annual precipitation and the slope of the terrain. The most important types of habitats (types of KVES) for orchids in Czechia are oak and oak-hornbeam forests, followed by agricultural meadows (Paper V). By this, we can improve management plans that are crucial for maintaining orchid localities.

ABSTRAKT

Přírodní prostředí se v posledních desetiletích významně změnilo, především kvůli intenzivní činnosti člověka. Existují důkazy pro to, že teď nejspíš čelíme šestému velkému vymírání druhů a vhodné areály druhů se zmenšují. Proto se také populace mnoha rostlin a živočichů zmenšují a mnohé z nich dokonce vymřely. My jsme naši pozornost zaměřili na orchideje, protože jejich rozšíření vykazuje jeden z nejvyšších poklesů mezi všemi rostlinami.

Tato práce se zabývá bohatostí druhů a rozšířením orchidejí, mírou a příčinami jejich velkého poklesu a vymírání, a kromě toho i faktory, které ovlivňují jejich výskyt v České republice a v Řecku. Ve většině předložených studií jsme využili databázi Agentury ochrany přírody a krajiny České republiky, která obsahuje více než 115 000 údajů o výskytu orchidejí v ČR. Typy rozšíření orchidejí jsme analyzovali v šesti rozdílných floristických oblastech, které se liší nadmořskou výškou a složením tamní flóry. Hlavní výsledky jsou shrnuty níže:

- Speciální strategie opylování orchidejí, stejně jako typ jejich kořenů v České republice i v Řecku hrají roli při rozšíření orchidejí ve zmíněných dvou zemích (Studie I, II a VI). Navíc jsme zjistili, že typy rozšíření se liší mezi šesti zkoumanými floristickými regiony (Studie I a II). V České republice jsou nejrozšířenější skupinou orchideje s oddenky, naopak v Řecku jsou nejčastější orchideje s hlízami (Studie I a VI). Domníváme se, že tyto rozdíly v rozšíření orchidejí by mohly být založeny na orografii zmíněných zemí, rozšíření biotopů vhodných pro výskyt orchidejí a typu podloží.
- Největší pokles v rozšíření orchidejí ve sledovaných obdobích byl zjištěn pro kriticky ohrožené druhy České republiky (Studie III). Bohužel, počet lokalit vhodných pro výskyt českých orchidejí klesl o 8 až 92 % v závislosti na druhu (Studie IV). Jeden z nejohroženějších druhů orchidejí české flóry je švihlík krutiklas (*Spiranthes spiralis*). Výskyt orchidejí v České republice je ovlivněn zejména rozšířením jejich vhodných biotopů.
- Nejdůležitějším faktorem, který ovlivňuje rozšíření orchidejí v Jihočeském kraji, je vegetační pokryv, v našich studiích vyjádřených konsolidovanou vrstvou ekosystémů (KVES). Dalšími důležitými faktory jsou roční průměrné množství srážek a sklon svahu na lokalitě. Nejvýznamnějším typem vegetačního pokryvu (habitatu) pro výskyt českých orchidejí v krajině jsou dubové a dubovo-habrové lesní porosty následované kulturními loukami, které jsou obhospodařovány místními zemědělskými družstvy (Studie V). Díky těmto zjištěním se může zlepšit cílený management, který je zásadní pro zachování vhodného stavu orchidejových lokalit.

INTRODUCTION

Nowadays, we hear everywhere that a drastic decrease of biodiversity is occurring. The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), working under the UN auspices, published an extensive report about global assessment of plant and animal biodiversity in May 2019 (https://www.ipbes.net/global-assessment). According to this report, we are facing the sixth global extinction of species, species diversity in decreasing worldwide at a fast pace, the rate of species extinction is now hundred times higher than the average for the last ten million years and one-eighth of existing species is endangered (https://ipbes.net/global-assessment). Furthermore, the report of IPBES states that approximately three quarters of terrestrial and two thirds of marine environment were significantly altered by human activity. One of the main reasons that are responsible for the huge decrease of biodiversity in the world is loss of natural habitats of plants and animals (https://ipbes.net/global-assessment).

Orchids are known from all over the world because of their beautiful flowers in the wild, as well as in our gardens and homes and they became very popular in the last few decades. There are many publications on the distribution of orchids from all over the world, which indicate that both professionals and the lay public are interested in orchids (e.g. Millar 1978; Seidenfaden and Wood 1992; Bose et al. 1999; Dykyjová 2003; Vlčko et al. 2003; Jersáková and Kindlmann 2004; Průša 2005; Averyanov et al. 2015; Antonopoulos and Tsiftsis 2017; Tsiftsis and Antonopoulos 2017; Grulich 2017; Kühn et al. 2019; Knapp et al. 2020; Wagensommer et al. 2020 and many others). Unfortunately, the family of Orchidaceae is one of the most threatened plant families showing a high risk of species extinction (Swarts and Dixon 2009). Orchids are disappearing worldwide, mostly due to habitat loss, but other factors like climate change are likely to increase in importance during the 21st century (Wotavová et al. 2004, Pfeifer et al. 2006). Because of the high risk of extinction, orchids are listed in CITES and protected by law in many countries in the world. All aspects that will be mentioned below make orchids an excellent plant family for various studies from the point of view of many branches of biology.

Orchids and their specialized life strategies

Orchids, with approximately 28 500 species (Govaerts 2020) are the most diverse and widespread family of flowering plants (Swarts and Dixon 2009) and are classified among the most threatened groups worldwide (Cribb et al. 2003; Kull and Hutchings 2006). They are an ideal group for exploring determinants of species diversity. This is because of activities of professionals and amateurs causing that orchids are well recorded and studied in many countries in Europe (Kull et al. 2006).

Most species of orchids are threatened in the wild (Cribb et al. 2003) and are disappearing from their natural habitats worldwide (Cribb et al. 2003; Kull and Hutchings 2006; Knapp et al. 2020; Wagensommer et al. 2020). In Europe, all orchids are terrestrial and can be found in almost all habitat types (Hágsater and Dumont 1996; Delforge 2006; Štípková et al. 2017). The most species-rich area in Europe is Southern Europe, especially the Mediterranean (Del Prete and Mazzola 1995; Hágsater and Dumont 1996). Certain orchid genera (e.g. *Ophrys*, *Serapias*), for which Mediterranean is a centre of evolution, reach here a remarkable species diversity (Del Prete and Mazzola 1995; Phitos et al. 1995; Pridgeon et al. 2001), whereas species-rich genera of more northern origin (e.g. *Epipactis*, *Dactylorhiza*) reach their highest species diversity in Central and Northern Europe (Averyanov 1990). The availability of detailed records provide opportunities for comparative analyses of species declines over time. Therefore, it is a pity that despite the high number of studies dealing with orchids, we still lack rigorous analyses of this data aimed at determining the relative importance of environmental factors and species traits associated with the decline in numbers of orchid sites and species.

There is an important life history trait that plays a significant role in determining orchid presence/absence and distribution in space: their specific **rooting system**, which is thought to represent particular strategies for underground storage of resources (Rasmussen 1995). In some species, the root system consists of a simple rhizome, whereas in others it is thicker and tuberous and serves as a storage organ. Coarse division of the European orchids in terms of their root systems could be useful for testing hypotheses of distribution patterns, as this trait has evolved and differentiated in response to changing climatic conditions (Averyanov 1990).

Following approaches on the evolutionary trends of the temperate orchids (Dressler 1981, Averyanov 1990, Tatarenko 2007), the species of orchids have been classified in three categories in this thesis. The classification was based on the above-mentioned morphology of their root system, which also demonstrates how primitive or highly evolved the orchid species in question is. Based on these classification criteria, the first species group consists of the rhizomatous orchids (*Cephalanthera*, *Corallorhiza*, *Cypripedium*, *Epipactis*, *Epipogium*, *Goodyera*, *Hammarbya*, *Limodorum*, *Liparis*, *Malaxis*, and *Neottia*). The second species group consists of orchids with palmate or fusiform tubers, which represent an intermediate stage (hereafter called as intermediate) in the evolution of the temperate orchids of Eurasia, and as a result, this group includes the species of the genera *Dactylorhiza*, *Gymnadenia*, *Platanthera* and *Pseudorchis*. The third species group consists of those orchids having spheroid or spindle-shaped tuberous root system (*Anacamptis*, *Herminium*, *Himantoglossum*, *Neotinea*, *Ophrys*, *Orchis*, *Spiranthes* and *Traunsteinera*).

Relationship of species richness of orchids with different rooting systems with various ecological factors and rate of specialization based on specific environmental conditions have not been studied in Europe before. To fill this gap in our knowledge, we explored the associations of orchid species richness and the degree to which an orchid species is specialized to specific environmental conditions (measured as species specialization index) with altitude in the Czech Republic (Paper I) and with various ecological factors in Greece (Paper VI).

In addition to their specific rooting systems, orchids have very complicated **pollination strategies**. Survival of an orchid population or even a species may strongly depend on pollination and subsequent seed production (Jacquemyn et al. 2005a). As specialized pollination systems may be particularly vulnerable to anthropogenic landscape modification (Anderson et al. 2011; Pauw and Bond 2011; Phillips et al. 2015), the type of pollination system may strongly affect species survival.

Generally, orchids are characterized by a diversity and specificity of pollination mechanisms, which may involve food-foraging, territorial defence, pseudoantagonism, rendezvous attraction, brood-site and shelter imitation, sexual response, or habitat-selection behaviour of their pollinators (Ackerman 1986; Tremblay 1992; Tremblay et al. 2005; Jersáková et al. 2006; Micheneau et al. 2009). Most plants pollinated by animals produce and offer rewards to attract pollinators to visit their flowers (nectariferous species; Simpson and Neff 1983). Nectar is considered the most common floral reward (Dressler 1981; Jersáková and Johnson 2006) and can influence several aspects of pollinator behaviour (Jersáková and Johnson 2006). However, some plants attract pollinators, although they do not offer them any reward in their flowers (nectarless – often also called deceptive – species; Heinrich 1979; Bell 1986). The nectarless strategy has evolved in many plant families, but most of nectarless species are orchids (Renner 2005; Jersáková et al. 2006). In general, plants of nectariferous species are visited more frequently than nectarless plants (Neiland and Wilcock 1998; Pellissier et al. 2010). Pollinators also visit more flowers per inflorescence in nectariferous than in nectarless species (Jersáková and Johnson 2006; Hobbhahn et al. 2017). Nectariferous species are less pollinator-specific than nectarless species, among which the most pollinator-specific are sexually deceptive species

(Cozzolino and Widmer 2005; Phillips et al. 2009). As much as 60–70% of orchids have a single pollinator species (Tremblay et al. 2005). This specialization for a single or a few pollinators (Tremblay 1992; Phillips et al. 2009) makes orchids vulnerable to fluctuations in pollinator abundance. Nectariferous orchids are better competitors for pollinators than nectarless orchids (Pellissier et al. 2010). All this has consequences for fruit production and therefore fitness of the plants. As a result, nectariferous species have a higher fruit set than nectarless ones (Neiland and Wilcock 1998; Tremblay et al. 2005; Phillips et al. 2009; Hobbhahn et al. 2017) in all geographical areas (Neiland and Wilcock 1998) due to pollination limitation (Neiland and Wilcock 1998; Tremblay et al. 2005). According to facts mentioned above, we suppose that pollination strategy plays a role in orchid distribution (Paper II).

All the above affect the altitudinal and spatial distribution of orchids, as well as a range of ecological conditions. For example, on La Reunion Island, Jacquemyn et al. (2005b) report that animal-pollinated orchids are more abundant at lower altitudes, while at high altitudes orchids tended to be auto-pollinated and cleistogamous. In Switzerland, the relationship between altitude and frequency of orchids of different reward strategies indicates a significant decrease in the occurrence of generalized nectarless species of orchids with increase in altitude (Pellissier et al. 2010).

In addition to the pollination strategy, pollinator abundance can also affect fruit set in orchids. Pollinator abundance is influenced by climate (temperature, seasonality) in a given area, which in turn is strongly determined by altitude (Arroyo et al. 1982; Körner 2007). Although hypotheses testing associations of species richness and niche breadth with altitude are frequently referred to in the literature (e.g. Kluge and Kessler 2011; McCreadie et al. 2017; Herrera et al. 2018; Vargas et al. 2018 and so on), none of these studies distinguished between pollination strategies (nectariferous/nectarless).

Orchids and their conservation

One of the key goals of conservation biology is to determine what causes declines in biodiversity and suggest ways of stopping or slowing them down (Gaston and Blackburn 2000). This is especially true in Europe, where the numbers of species, abundances and distributions of many plant and animal species have dramatically declined during recent decades.

The need for taking effective conservation measures is urgently required for areas and countries that have been affected by **human activities in the past decades**, and thus have lost a part of their biodiversity or their species distributions have been largely diminished (Paper III and Paper IV). It is commonly accepted that urbanization, land use changes and intensification of agriculture have resulted in a dramatic loss of habitats and fragmentation (Stewart 1992; Fischer and Stöcklin 1997; Kull et al. 2002, 2016; Bilz et al. 2011; Tsiftsis et al. 2011). The current landscape in Europe is mainly a result of the changes in farm management that occurred over recent decades (Henle et al. 2008). This affected the composition of the flora and fauna in most areas and resulted in a decline in European biodiversity (Fahrig et al. 2011; Ferreira et al. 2013; Brunbjerg et al. 2017; Fardila et al. 2017; Poschlod and Braun-Reichert 2017; Hass et al. 2018; Kurze et al. 2018). As for most other taxonomic groups, the reasons for the decline in orchid biodiversity include habitat loss, eutrophication and fragmentation (Wotavová et al. 2004; Janečková et al. 2006; Kull and Hutchings 2006; Kull et al. 2016). Central European countries have been intensively affected by land use change or agricultural intensification. Among these countries, the Czech Republic was strongly affected by such changes over the last few decades (Paper III). In the past, there were important changes in the use of land in the Czech Republic, which differed from those that occurred in western parts of Europe because of the differences in the political regimes (Adams and Adams 1971; Wädekin 1982; Krčmářová and Jeleček 2017). Before 1948, fields and meadows were traditionally managed (Krčmářová and Jeleček 2017), which involved mowing and grazing, low intensity agriculture of small fields and low application of fertilizers (Adams and Adams 1971). After 1948, small fields were consolidated into huge fields (Skaloš et al. 2011) and subsidies for fertilizers were provided, which resulted in the amount of chemicals in the soil increasing rapidly (Adams and Adams 1971). As a result, many orchids declined and can only be found at a small number of sites (Paper IV). After the change of regime in 1989, the subsidies for fertilizers ceased, which resulted in a great decline in the use of fertilizers for a while (Reif et al. 2008). The implications for the survival of orchid sites were not dramatic, however (Paper IV).

The knowledge of orchid ecology, including environmental gradients that influence the patterns in orchid abundance, distribution, richness and composition, is essential for planning and applying conservation strategies and actions (Tsiftsis et al. 2008; Swarts and Dixon 2009), as lack of such knowledge negatively affects our ability to identify sites that are worth protecting.

Orchid distribution patterns

Understanding the abundance and distribution patterns of species at large spatial scales is one of the key goals of biogeography and macroecology (Brown 1995; Gaston and Blackburn 2000; Paper VI), but effective conservation requires knowledge of species at small spatial scales (Tsiftsis et al. 2008; Swarts and Dixon 2009).

Species richness decreases from the equator towards the poles (Crame 2001; Francis and Currie 2003), and this pattern is among the most consistent ones in biogeography (Hillebrand 2004). The dependence of species richness on elevation is usually hump-shaped (Vetaas and Grytnes 2002; Bhattarai and Vetaas 2003), or monotonically decreases with increasing elevation (Bachman et al. 2004; Jacquemyn et al. 2005b), but sometimes species richness increases with elevation or shows an inversely unimodal trend; more rarely no obvious trend can be observed (Grytnes 2003; Hrivnák et al. 2014). In temperate regions, plant species richness is lower in areas of cold compared to warm climatic conditions, while species niches and range sizes tend to be broader (Stevens 1989; Thompson 2005). However, except of the environmental gradients, other important factors are also influencing patterns and rates of niche breadth, e.g. the life-history strategy of the studied species group (Kostikova et al. 2013). Global warming has a direct effect on species distributions, as over the last years an increasing number of plant species occurring in the high mountains of Europe has been observed (Steinbauer et al. 2018). Although some species expand their distribution ranges towards northern areas or to higher elevations, other species are becoming more restricted due to the desertification observed in the southern parts of Europe (Karamesouti et al. 2015).

Species distribution models (**SDMs**) are a useful tool, which is often applied in many branches of biogeography, conservation biology, and ecology in the last decades (Elith and Leathwick 2009), especially when threatened species are concerned (Guisan et al. 2013). These numerical tools combine species occurrence records with environmental data (Elith and Leathwick 2009). In combination with GIS techniques, these models are especially important and useful for predicting occurrence of rare species (Guisan and Thuiller 2005). Although the results of species distribution models often suffer from high levels of uncertainty of several factors, concerning biased species distribution data, errors in environmental variables used as predictors, spatial resolution, and the modelling process (Elith and Graham 2009; Rocchini et al. 2011), SDMs have become widely accepted tools to predict species distributions (Tsiftsis et al. 2012).

The maximum entropy algorithm in the **MaxEnt** application (Elith et al. 2006; Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011) is often used for modelling species distributions from presence-only species records (Elith et al. 2011). This approach was used by conservation practitioners for predicting the distribution of a species from a set of occurrence records and environmental variables (Elith et al. 2011; Fourcade et al. 2014). MaxEnt is one of the most robust approaches of species distribution in terms of successfully estimating the area from only a few records of occurrence (Hernández et al. 2006; Yi et al. 2016). Despite long history of studies on orchids, only a minute part of previous papers concerning distribution, phytogeography, or conservation strategies of this taxonomic group included application of species distribution models (e.g., see Kolanowska 2013; Wan et al. 2014; Reina-Rodríguez et al. 2016; Vollering et al. 2016). Presence-only modelling methods require exclusively a set of known species occurrences together with predictor variables such as topographic, climatic, edaphic, biogeographic, and/or remotely sensed data (Phillips et al. 2006; Phillips and Dudík 2008). The above-mentioned tools help us with determining the suitable areas for orchid occurrence and factors that influence orchid distribution in the Czech Republic (Paper V).

Factors affecting orchid distribution

Questions concerning species diversity have attracted ecologists for over a century. Recently, this issue became even more important, because the diversity of life on Earth is in rapid decline (Dirzo and Raven 2003). Therefore, one of the most pressing tasks facing the global conservation community is trying to understand the main factors determining diversity of species (Possingham and Wilson 2005) and identifying important areas for their conservation (Tsiftsis et al. 2011). Orchids are also known for their sensitivity to environmental changes (Dirzo and Raven 2003), as well as to their high extinction risk, compared to other plant families, as a result of natural and/or anthropogenic causes (Hutchings 1989; Kull et al. 2006).

One of the most worrying issues is that we still do not know the optimal abiotic and biotic requirements for population persistence of many of orchid species (Swarts and Dixon 2017). There are only a few studies in the Czech Republic dealing with the factors that determine orchid presence/absence and distribution in space, and most of them include only one or a few species and/or a limited part of the distribution of the species studied (e.g. Štípková et al. 2017, 2018).

On a regional scale, geological substrate and the distribution of suitable plant communities determine the distribution of species (Tsiftsis et al. 2008), whereas on broad geographical scales, plant species richness is largely determined by climatic conditions (Sanders et al. 2007; Acharya et al. 2011; Trigas et al. 2013), which are in turn mostly influenced by elevation and latitude of the area considered.

A better understanding of how species richness, niche breadth and range size are associated with geographical and/or environmental gradients is of crucial importance for species conservation and may even help us to predict the effects of global change, specifically when orchid distribution is considered (Swarts and Dixon 2009; Zhang et al. 2015). In spite of many orchid atlases describing their distributions, there is only scattered information on the factors determining orchid distribution and species richness throughout the Czech Republic (Paper I and II).

AIMS OF THE STUDY

- To explore the factors determining orchid species richness and the rate of specialization to specific environmental conditions in different altitudes in the Czech Republic and Greece, based on specific life strategies of orchids: different types of orchid root systems (Paper I, VI) and different pollination strategies of orchids (Paper II).
- To assess the rate of extinction of Czech orchids based on the changes in land use and quantify the percentage decrease of the number of orchid sites in the Czech Republic based on different systems of agriculture in individual time periods (Paper III, Paper IV).
- To determine which environmental factors affect the distribution of selected orchid species and tried to find new localities for orchid occurrence in the area of South Bohemia in the Czech Republic, using potential distribution maps generated by the MaxEnt program (Paper V).

MATERIALS AND METHODS

The dataset of orchid records we used in our analyses in Papers I-IV was based on the database of the Nature Conservation Agency of the Czech Republic. Flora in the Czech Republic is not uniformly distributed and depends on the region. There are six phytogeographical regions in the Czech Republic that vary in their average altitude and are characterized by different composition of their flora. We always analysed particular factors in each of the six phytogeographical regions separately.

In **Paper I**, orchids were classified into one of three groups based on their rooting system (rhizomatous, intermediate and tuberous), whereas in **Paper II**, species were classified as nectarless or nectariferous based on their pollination strategy. Both papers followed the same procedures: we extracted the altitude of each orchid record from the altitudinal layer using the WorldClim database and divided them into 100-m vertical intervals in each of the six floristic regions. Then, we counted the number of orchid taxa occurring in each vertical interval for each orchid category. Finally, we calculated orchid density at each altitudinal interval and species specialization index for each orchid species. This process was followed for each phytogeographical region by considering all the orchids occurring in each site, as well as the 19 bioclimatic variables and altitude of a specific region. We used regression in order to explore the associations of orchid density and mean species specialization index with altitude. All analyses were performed in R and ArcGIS.

In **Paper III**, we categorized orchids as nectarless or nectariferous on the basis of whether or not they provide nectar to their pollinators. We considered three different periods to address the two substantial shifts in land use in the Czech Republic in 1948 and in 1989. We compared historical and recent data on species occurrences for 63 species of Czech orchids in the three periods. We performed all analyses in three different spatial resolutions (1 × 1 km, 5 × 5 km and 10 × 10 km), to explore whether grid cell size affects the interpretation of our results. We used ArcMap to create the three datasets corresponding to the three spatial resolutions and we performed all further analyses using R.

In **Paper IV**, we created a grid of 1 × 1 km squares from orchid records mentioned above. For each orchid site, we determined the latest year when orchids were still present at the site. If the year was 1990 or later, the site was considered as still occupied. If the last record of an extant population at a site was prior to 1990, this date was considered to be the date of extinction of the orchid population at the site. We classified orchids into threat categories based on the latest Red List classification of the Czech Republic. We analysed only species listed in the extinct (A1) and critically endangered (C1) categories, in total 34 species. We categorized the A1 and C1 species according to the number of sites recorded in the database and considered species of *Epipactis* as a special case. For each species, we calculated the number of sites at which extinction was recorded during the selected time periods.

In **Paper V**, we used data about orchid occurrence from five databases (with no public access) deposited in České Budějovice, in the Global Change Research Institute. We visited all localities (total of 428 sites) mentioned in the database in the region of South Bohemia during 2014 – 2016 for all studied squares of the Czech network mapping. We wanted to determine, whether a selected orchid species is still present at a particular locality or whether it has disappeared there. If an orchid species was found, we recorded information such as number of flowering individuals, accurate GPS position of the locality, health state of the locality and if the locality is managed or not. We analysed seven orchid species and chose a set of possible important environmental variables according to our knowledge from various studies and information from the literature that possibly affect the distribution of studied species. We used MaxEnt program based on the species presence-only observations and environmental data from WorldClim database at a spatial resolution of 500 m.

In **Paper VI**, the area of Greece was divided into 2047 grid cells, size of each grid cell was 10 × 10 km. Based on occurrence data obtained from Dr. Tsiftsis and his colleague, we determined presence/absence of each orchid species in each of the 1741 grid cells in areas where orchids occur. We divided orchids into three categories based on the morphology of their root system (rhizomatous, intermediate and tuberous) and used environmental variables important for Greek orchids based on the knowledge of Greek orchid specialists, elevation and three bioclimatic variables from the WorldClim database determined during the selective procedure. To explore the associations between species richness, mean niche breadth and mean distribution of the orchid groups and the selected predictors, we analysed the data using regression techniques. We performed analyses in R, PASW and used ArcGIS.

RESULTS AND DISCUSSION

In **Paper I**, the highest species density in the Czech Republic was recorded between 300 and 900 m, which could be attributed to the fact that the distributions of many species of orchids overlap at these altitudes. The most widely distributed group are the rhizomatous orchids, followed by intermediate orchids. In the Czech Republic, the middle and high altitudes are abundantly covered by forests, where most orchids from the previously mentioned groups typically occur. The least widely distributed group is that of tuberous orchids, whose centre of evolution and the highest species richness is in southern Europe. The trends in both species richness and mean species specialization index differed between the six floristic areas of the Czech Republic within each of the three orchid groups studied. We assume that these differences in the trends might be based on the orography of the country, distribution of suitable habitats and types of bedrock, together with availability of proper mycorrhizal fungi, at different altitudes in the Czech Republic.

In **Paper II**, we found that there are more nectariferous than nectarless species of orchids in the Czech Republic, which is consistent with other published studies. We detected differences between the six different regions in Czechia in terms of numbers and density of the studied orchid species. The trends in species density of both nectarless as well as nectariferous orchids were very similar in all floristic regions. We assume the trends strongly depend on the distribution of different habitats and availability of pollinators. We suppose that the association of altitude with the richness of orchid flora is much stronger than that with the biogeography. We suggest that particular attention should be also paid to the biology and requirements of the plant-pollinator relationships.

In **Paper III**, we found that many species of orchids suffered a rapid decline in their distribution in the Czech Republic during the three time periods studied. The highest decline in distribution was recorded for critically endangered taxa (C1) of both nectariferous as well as nectarless orchids. The highest decline was observed for *Anacamptis coriophora* and S*piranthes spiralis* (nectariferous orchids) and for *Himantoglossum adriaticum* (nectarless orchids). Orchids in the Czech Republic were intensively affected both by the agricultural intensification and specific changes in forest management practices. The distribution of orchids is mainly affected by the distribution of their habitats. One of the main reasons for orchid decline is artificial changes of natural habitats, mainly due to changes in agricultural practices in the Czech Republic. We concluded that the spatial resolution used in analyses is very important for results interpretation and emphasized that authors should use the most precise spatial resolution available to avoid misinterpretation of their results.

In **Paper IV**, we found that the vast majority of orchids in the Czech Republic disappeared from many of their historical localities during all time intervals analysed. The number of sites that are suitable for the Czech orchids declined by 8–92%, depending on the species. Moreover, four species became extinct from the Czech orchid flora. We also determined that the most threatened orchids in Czechia are *Spiranthes spiralis*, *Anacamptis palustris*, *Epipogium aphyllum* and *Goodyera repens*. These species are vanishing because of the excessive use or alteration of their natural habitats, mainly caused by the human impact. The extinction and dramatic decline of orchids in the Czech Republic seems to be closely related with changes in agricultural practices in the open, as well as in forest habitats. We concluded that preserving suitable orchid habitats seems to be the key for keeping Czech orchid flora alive.

In **Paper V**, we proved that the amount of arable land is an important factor that has a negative effect on the distribution of the orchid species studied, as was also mentioned in other studies. We determined that the most important environmental factor affecting the distribution of numerous Czech orchids in the region of South Bohemia was the land cover, expressed as the consolidated layer of ecosystems (KVES). The other two important environmental predictors were the mean annual precipitation and the slope of the terrain. We also evaluated the most important types of habitats (types of KVES) for orchids. Based on our results, these were the habitats of oak and oak-hornbeam forests followed by cultural meadows. Moreover, there are still places which are highly suitable for orchid occurrence based on the potential distribution maps of studied species and a possible finding of a new locality is highly probable in such places.

In **Paper VI**, contrary to results in Paper I from the Czech Republic, the most widely distributed orchids in Greece were the tuberous orchids, followed by rhizomatous and intermediate ones. The distributions of rhizomatous and intermediate orchids are mainly associated with the orographic configuration of Greece, whereas the tuberous orchids are widely distributed in the southern, central and north-western areas of Greece. Spatial distribution of Greek orchids is associated with a combination of elevation, latitude and climate. Species richness for the three belowground (root system) strategies was significantly affected by the predictors, whereas their mean niche breadth and mean distribution were largely dependent on their evolutionary history expressed by the root system. The maximum elevation was the most significant factor for the rhizomatous and intermediate orchids, whereas minimum temperature in the coldest month was highly significant for the tuberous orchids. Our study demonstrates that the number of tuberous orchid species declines with increasing latitude in Greece, contrary to the other two groups. The patterns along the latitudinal gradient can be attributed to the ecological requirements, different origin and evolutionary history of the orchid genera forming each orchid group.

CONCLUSIONS

In the papers mentioned above, we presented a new insight into facts that affect orchid life. Although the majority of studies was performed in the Czech Republic, we believe that our results and subsequent suggestions are also applicable in other parts of Central Europe, as well as in other temperate regions. The key conclusions are as follows:

- The distribution of orchid taxa with both different root systems (Paper I) and pollination strategies (Paper II) in the Czech Republic strongly depends on the distribution of suitable habitats and bedrock types, together with mycorrhizal fungi, at different altitudes in the country. The association of altitude with the richness of orchid flora in the Czech Republic is much stronger than that with the biogeography. On the contrary, the patterns in the distribution of Greek orchid taxa with different root systems are associated with geology and the special topography (particularly in terms of elevation, latitude and climate) as well as with the biogeography of the area (Paper VI).
- The distributions of many species of Czech orchids have decreased markedly over time. We assumed that these changes are directly associated with changes in agriculture practices in the Czech Republic and abandonment of traditional management. We suggest that authors should use the most precise spatial resolution available in order to avoid misinterpretation of their results (Paper III). We found that the vast majority of orchids disappeared from many of their historical localities and four orchid species became extinct. The most threatened orchid species in the Czech Republic is *Spiranthes spiralis* (Paper IV). All these changes seem to be closely related with changes in agricultural practices and excessive use or alteration of orchid natural habitats. We believe that our results can be used to set up specific conservation measures that are needed either to prevent further orchid decline or to the recovery of specific orchid populations.
- The most important factor that affects the distribution of many orchids in the South Bohemian region is the land cover, expressed by the consolidated layer of ecosystems (KVES). Thanks to potential distribution maps, we found other places with suitable environmental conditions for possible orchid presence (Paper V). The findings may help in the field of orchid conservation by protecting natural habitats with suitable environmental conditions for orchid species.

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PARTICIPATION IN INTERNATIONAL ORCHID CONFERENCES

2019: International Orchid Conference & Workshops for Young Scientist, Spała, Poland, September 24-28 (oral contribution: *How can species distribution models help us with determining areas of special interest for orchid diversity in Colombia?* – **received an award as the best student presentation**); VI Scientific Conference on Andean Orchids, Medellin, Colombia, August 6-9 (poster presenter); 7th International Orchid Conservation Congress, Kew, Great Britain, May 28-June 1 (oral contribution: *Impact of root system type and elevation on the richness and distribution of orchid flora in the Czech Republic*)

2018: 6th International Orchid Workshop, Białystok, Poland, May 28- June 1 (oral contribution: *Factors associated with the distribution of orchids in the Czech Republic and their comparison from two different regions*)

2017: 22nd World Orchid Congress, Guayaquil, Ecuador, November 8-11 (oral contribution: *Application of species distribution models on orchid data from Colombia*)

2016: 6th International Orchid Conservation Congress, Hong Kong, China, May 16-20 (poster presenter)

2015: V Scientific Conference on Andean Orchids, Santiago de Cali, Colombia, November 19-21 (poster presenter); International Conference on Temperate Orchids: Research &

Conservation, Samos Island, Greece, April 13-19 (oral contribution: *Determinants of orchid species diversity*)

2011: 4th International Orchid Conservation Congress, Hluboká nad Vltavou, Czech Republic, May 29-June 6 (poster presenter)

PARTICIPATION IN INTERNATIONAL APHID CONFERENCES

2019: 6th International Entomophagous Insect Conference, Perugia, Italy, September 9-13 (oral contribution: *How much is aphid population dynamics affected by their natural enemies?*)

2018: Benefits and risks of exotic biological control agents, IOBC-WPR Working Group Meeting, Ponta Delgada, Azores, September 12-14 (oral contribution: *How much is aphid population dynamics affected by their natural enemies? A Greek example.*)