FACTORS DETERMINING THE DISTRIBUTION OF ORCHIDS – A REVIEW WITH EXAMPLES FROM THE CZECH REPUBLIC

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ABSTRACT

The natural environment has been significantly altered by human activity over the past few decades. There is evidence we are now experiencing the sixth mass extinction, as many species of plants and animals are declining in abundance. We focused on the Orchidaceae because this plant family has experienced one of the biggest reductions in distribution. We investigated patterns in species richness and distribution of orchids, the rate and causes of their decrease and extinction, and factors influencing their occurrence in the Czech Republic and Greece. The key findings are: (i) Method of pollination and type of rooting system are associated with their distributions and they are different in the two countries. We assume that these differences might be due to the difference in the orography, distribution of suitable habitats and types of bedrock in these two countries. (ii) The greatest reduction in distribution was recorded for critically endangered taxa of orchids. The number of sites suitable for orchids in the Czech Republic declined by 8–92%. The most threatened orchid species are *Spiranthes spiralis*, *Anacamptis palustris*, *Epipogium aphyllum* and *Goodyera repens*. The distribution of orchids in the Czech Republic is mainly determined by the distribution of their habitats. (iii) The most important factor affecting the distribution of Czech orchids in South Bohemia is land cover. And the most important types of habitats (types in KVES) are oak and oak-hornbeam forests and agricultural meadows. Based on this information, it should be possible to improve the management that is crucial for maintaining orchid localities.

Keywords: decline; environmental factors; extinction; Maxent; orchids; pollination; root system

Introduction

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

Orchids are known all over the world because of their beautiful flowers in the wild, as well as in our gardens and homes, and have become very popular in the last few decades. There are many publications on the distribution of orchids worldwide, 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; Grulich 2017; Tsiftsis and Antonopoulos 2017; Kühn et al. 2019; Knapp et al. 2020; Wagensommer et al. 2020 and many others). Unfortunately, the family Orchidaceae is one of the most threatened plant families with 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.

Despite the high number of studies on orchids, we still lack critical information necessary for the conservation of Orchidaceae, especially for species that are known to be threatened or endangered. All aspects that will be mentioned below make orchids an excellent plant family for various studies on various aspects of biology.

Orchids and their Specialized Life Strategies

The orchid family is an important group with respect to conservation biology (Pillon and Chase 2006), because so many are threatened with extinction (Swarts and Dixon 2009). Many characteristics, such as great species richness, specific role in ecosystems, or threat of extinction, make it crucial to explore the distribution and conservation status of Orchidaceae (Zhang et al. 2015).

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

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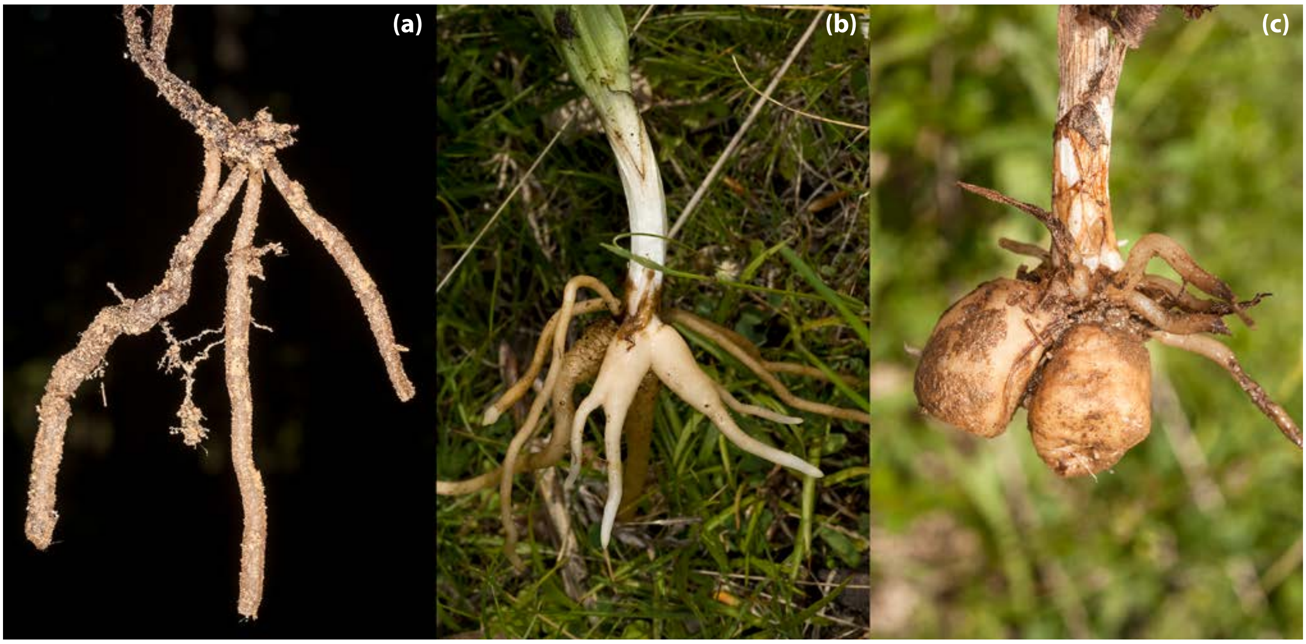

Fig. 1 Different types of orchid rooting systems: (a) rhizomatous, (b) intermediate and (c) tuberous.

ideal group for exploring determinants of species diversity because they 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 habitats (Hágsater and Dumont 1996; Delforge 2006; Štípková et al. 2017). The most species-rich area in Europe is Southern Europe, especially the Mediterranean area (Del Prete and Mazzola 1995; Hágsater and Dumont 1996). Certain orchid genera (e.g. *Ophrys*, *Serapias*), for which the Mediterranean area is a centre of evolution, are remarkably species diverse (Del Prete and Mazzola 1995; Phitos et al. 1995; Pridgeon et al. 2001), whereas the greatest species diversity of species-rich genera are of more northern origin (e.g. *Epipactis*, *Dactylorhiza*) is recorded in central and northern Europe (Averyanov 1990). The availability of detailed records provides opportunities for comparative analyses of the declines in species 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 the numbers of sites suitable for orchids and particular species. However, such an analysis is crucial for their conservation in terms of an effective management of orchid sites (Kull and Hutchings 2006). Terrestrial orchids are probably one of the best examples of the decline in biodiversity in plants.

There is an important life history trait that plays a significant role in determining orchid presence/absence and distribution in space: their **rooting system**, which is thought to represent particular strategies for underground storage of resources (Rasmussen 1995). In some species, the rooting system consists of a simple rhizome, whereas in others it is thicker and tuberous and serves as a storage organ. Among the European orchids, the genera *Epipactis*, *Cephalanthera* and *Cypripedium*, which are believed to be the most primitive, have short rhizomes. The most important evolutionary development in the growth forms of Orchidaceae was the production of efficient storage organs (tuberoids). In this evolutionary process, *Pseudorchis albida* is the most primitive tuberoid orchid, whereas the palmate tuberoids (*Dactylorhiza*, *Coeloglossum*, *Gymnadenia*) and those with fusiform tubers (e.g. *Platanthera*) evolved later (Dressler 1981; Averyanov 1990; Tatarenko 2007). Coarse division of the European orchids in terms of their rooting systems could be useful for testing hypotheses on their patterns of distribution, as this trait has evolved and differentiated in response to changing climatic conditions (Averyanov 1990).

Following the evolutionary trends in temperate orchids (Dressler 1981; Averyanov 1990; Tatarenko 2007), the species of orchids were classified here in three categories based on the above-mentioned morphology of their root system, which also indicates how primitive or highly evolved an orchid is. Based on this classification, the first species group consists of the rhizomatous orchids (*Cephalanthera*, *Corallorhiza*, *Cypripedium*, *Epipactis*, *Epipogium*, *Goodyera*, *Hammarbya*, *Limodorum*, *Liparis*, *Malaxis* and *Neottia*), the second, those with palmate or fusiform tubers, which is the intermediate stage (hereafter referred to as intermediate) in the evolution of temperate orchids in Eurasia, and includes species of the genera *Dactylorhiza*, *Gymnadenia*, *Platanthera* and *Pseudorchis*. The third species group consists of those orchids with a spheroid or spindle-shaped tuberous root system (*Anacamptis*, *Herminium*, *Himantoglossum*, *Neotinea*, *Ophrys*, *Orchis*, *Spiranthes* and *Traunsteinera*). See Fig. 1 for illustrations of these categories.

Relationship between species richness of orchids with different rooting systems and various ecological factors and degree of specialization based on specific environmental conditions have not been previously studied in Europe. To fill this gap in our knowledge, we explored the associations of orchid species richness and the degree to which an orchid species is adapted to living in specific environmental conditions (in terms of species specialization index) with altitude in the Czech Republic (Štípková et al. 2021a) and with various ecological factors in Greece (Tsiftsis et al. 2019).

In addition to the differences in their 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 modification of landscapes (Anderson et al. 2011; Pauw and Bond 2011; Phillips et al. 2015) and may strongly affect species survival.

Generally, orchids are characterized by a diversity and specificity of pollination mechanisms, which may involve the 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 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, but do not offer any reward (nectarless – often also called deceptive – species; Heinrich 1979; Bell 1986). The nectarless strategy has evolved in many plant families, but most 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 of nectariferous than 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 many as 60–70% of orchids have a single species of pollinator (Tremblay et al. 2005). This level of specialization (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 the 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). Based on the above, we propose that pollination strategy plays a role in orchid distribution (Štípková et al. 2020b).

All the above and a range of ecological conditions affect the altitudinal and spatial distribution of orchids. For example, on La Reunion Island, Jacquemyn et al. (2005b) report that animal-pollinated orchids are more abundant at lower altitudes, whereas at high altitudes orchids tended to be auto-pollinated and cleistogamous. In Switzerland, the relationship between altitude and frequency of orchids with different reward strategies indicates a significant decrease in the occurrence of 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 the climate (temperature, seasonality) in a given area, which in turn is strongly determined by altitude (Arroyo et al. 1982; Körner 2007). Although the testing of the 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. 2008 and so on), none of these studies distinguish between pollination strategies (nectariferous/nectarless).

Mycoheterotrophy allows orchids to adapt to a wide variety of habitats, even those with extreme conditions (e.g. sites with little soil or lack of light). In the upper mountain zone, although it rains equally all year round the upper soil horizons are rich in organic matter (mostly in forested habitats), orchids (mostly rhizomatous and to a lesser extent palmate or fusiform tuberoids) are adapted to the low light conditions, often involving obligate mycoheterotrophy (Jacquemyn et al. 2017). The tuberous orchids mostly occur in open, dry and hot environments around the Mediterranean and in nutrient poor and eroded soils (Averyanov 1990; Delforge 2006). Although in these areas, low availability of soil water and nutrients are causes of stress (contrary to light, which is the cause of stress in forested habitats), fungi provide orchids with the water and nutrients necessary for their survival and growth. Moreover, when conditions (e.g. climatic) are unsuitable, the underground organs of orchids can remain alive and dormant, exploiting fungi, for several years (Rasmussen 1995; Shefferson et al. 2018).

Orchids and their Conservation

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

The need for effective conservation measures is urgently required for areas and countries that were affected by human activities in past decades, and thus have lost a part of their biodiversity or the distributions of certain species have been greatly reduced (Štípková and Kindlmann 2021; Štípková et al. 2021b). It is commonly accepted that urbanization, land use changes and intensification of agriculture have resulted in a dramatic loss and fragmentation of habitats (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 recent changes in farm management (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 changes in land use or agricultural intensification. Among these countries, the Czech Republic was strongly affected by such changes during the last few decades (Štípková et al. 2021b). 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 due to changes 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 high levels of nutrient chemicals in the soil (Adams and Adams 1971). As a result, many orchids declined and can now only be found at a small number of sites (Štípková and Kindlmann 2021). After the change in regime in 1989, the subsidies for fertilizers ceased, which resulted for a while in a great decline in the use of fertilizers (Reif et al. 2008). The implications for the survival of sites suitable for orchids, however, were not dramatic (Štípková and Kindlmann 2021).

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), and lack of such knowledge negatively affects our ability to identify sites that are worth protecting. We also still lack the knowledge needed to develop management plans for orchids under current or future scenarios of habitat loss and climate change.

Among others, there are two crucially important values when orchid conservation and survival during climate change is considered: number of species per unit area and the degree to which an orchid species is specialized to specific environmental conditions. The former clearly determines the conservation value of an area, while the latter tells us how much a species may be endangered by changes in environmental conditions, e.g., climate change. Both values were used for assessing the factors that affect the distribution of Czech orchids (Tsiftsis et al. 2019; Štípková et al. 2020a; Štípková et al. 2021a).

Patterns in the Distribution of Orchids

Understanding the abundance and patterns in the distributions of species at large spatial scales is one of the key goals of biogeography and macroecology (Gaston and Blackburn 2000; Tsiftsis et al. 2019), 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 in biogeography (Hillebrand 2004). The dependence of species richness on altitude is usually hump-shaped (Vetaas and Grytnes 2002; Bhattarai and Vetaas 2003), or monotonically decreases with increasing altitude (Bachman et al. 2004; Jacquemyn et al. 2005b), but sometimes species richness increases with altitude or shows an inversely unimodal trend; more rarely there is no obvious trend (Grytnes 2003; Hrivnák et al. 2014). In temperate regions, plant species richness is lower in areas that are cold compared to those that are warm, while species niches and range sizes tend to be broader (Stevens 1989; Thompson 2005). However, in addition to environmental gradients, there are other important factors that influence these patterns and niche breadth, e.g. the life-history strategies of species (Kostikova et al. 2013). Global warming has a direct effect on species distributions, as over the last few years there has been an increase in the number of species of plant species occurring in high mountains in Europe (Steinbauer et al. 2018). Although distributions of some species now extend further north or to higher altitudes than previously, 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 over the last few decades were often used in many branches of biogeography, conservation biology and ecology (Elith and Leathwick 2009), especially in studies on threatened species (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 the occurrence of rare species (Guisan and Thuiller 2005). Although the results of species distribution models often suffer from high levels of uncertainty due to biases in 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 are nevertheless widely used 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 based on presence-only species records (Elith et al. 2011). This approach is 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 methods in terms of successfully estimating the area of distribution from only a few records of occurrence (Hernández et al. 2006; Yi et al. 2016). Despite the long history of studies on orchids, very few of the previous papers on the distribution, phytogeography, or conservation strategies for orchids are based on using 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 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; Štípková et al. 2020a).

Factors Affecting the Distribution of Orchids

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 the diversity of species (Possingham and Wilson 2005) and identifying important areas for conserving biodiversity (Tsiftsis et al. 2011). Orchids are also known to be affected by environmental changes (Dirzo and Raven 2003), as well as to their high risk of extinction, 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 species of orchids (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 the altitude and latitude of the area studied.

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 predict the effects of global change, especially when considering the distribution of orchids (Swarts and Dixon 2009; Zhang et al. 2015). In spite of the many atlases of the distributions of orchids, there is only scattered information on the factors determining orchid distribution and species richness throughout the Czech Republic (Štípková et al. 2020a; Štípková et al. 2021a).

Conclusions

In this review, we present a new insight into facts that affect orchid life. Although the majority of the studies are for the Czech Republic, we believe that our results and suggestions are also applicable to other parts of Central Europe, as well as other temperate regions.

The distribution of orchid taxa with different rooting systems and pollination strategies in the Czech Republic strongly depends on the distribution of suitable habitats and types of bedrock, 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 biogeography. On the contrary, the patterns in the distribution of Greek orchid taxa with different rooting systems are associated with geology and the special topography (particularly in terms of altitude, latitude and climate) as well as with the biogeography of the area.

The distributions of many species have decreased markedly over time. We assume 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. We found that the vast majority of orchids have disappeared from many of their historical localities and four orchids became extinct. The most threatened orchids in the Czech Republic are *Spiranthes spiralis*, *Anacamptis palustris*, *Epipogium aphyllum* and *Goodyera repens* (Štípková and Kindlmann

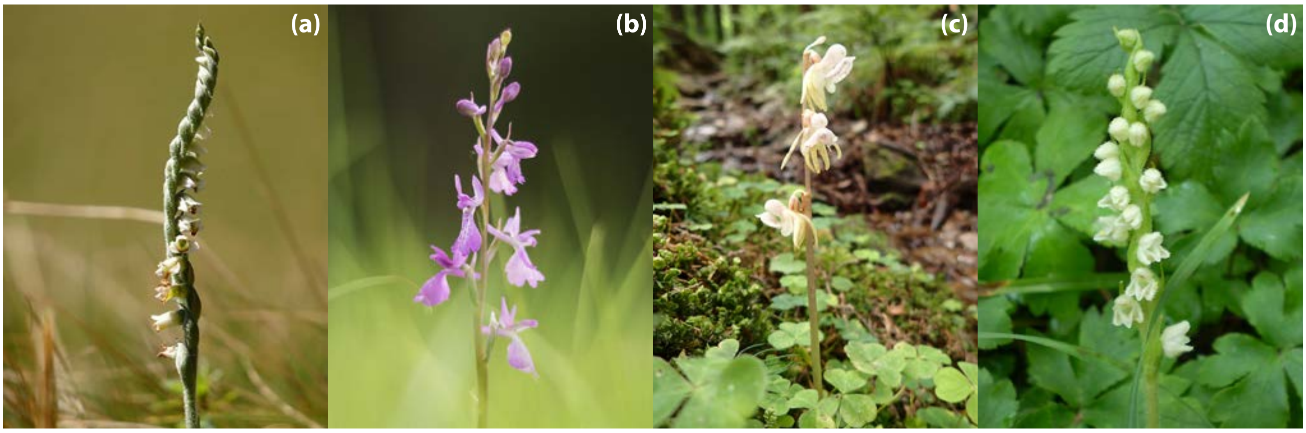

Fig. 2 Photographs of the most threatened species of orchids in the Czech Republic: (a) *Spiranthes spiralis*, (b) *Anacamptis palustris*, (c) *Epipogium aphyllum* and (d) *Goodyera repens* (a, c, d © Z. Štípková; b © J. Štěpán).

2021, Fig. 2). All these changes seem to be closely associated with changes in agricultural practices and in the use or alteration of orchid natural habitats. We believe that these results can be used to set up specific conservation measures that are needed either to prevent further decline in orchids or the recovery of specific orchid populations.

The most important factor that affects the distribution of many orchids in the South Bohemian region of the Czech Republic is land cover. Thanks to potential distribution maps, we found other places with suitable environmental conditions for orchids. These findings may help the conservation of orchids by protecting those habitats with suitable environmental conditions.

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