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Determinants of Orchid Occurrence: A Czech Example

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<http://dx.doi.org/10.5772/intechopen.74851>

Abstract

Orchids are an endangered plant group, protected in the whole world. Questions of their conservation are therefore highly discussed, but not all factors affecting their survival and distribution are known so far. The purpose of this study was to determine the environmental factors influencing the existence of certain orchid species in their localities in our model area – South Bohemia. Our data were analyzed using the MaxEnt program, which produces species distribution models (SDMs) and allows predicting potential occurrence of orchids in yet unknown localities. This program also determines the environmental factors affecting species presence. This is important for better protection of orchids, because only by knowing these factors, we can find new localities or improve management plans. We studied two orchid species growing in South Bohemia: *Dactylorhiza majalis* and *Platanthera bifolia*. The main factors affecting their occurrence were the consolidated layer of ecosystems, habitat heterogeneity, cover of arable land, and vertical heterogeneity. We determined areas, where new sites are most likely to be discovered and show them in the maps of the area. This approach can help in finding new localities of orchids and in understanding, which environmental factors influence the occurrence of these endangered orchid species.

Keywords: orchids, localities, database, species distribution models, MaxEnt

1. Introduction

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 [1, 2]. Therefore, one of the most pressing tasks facing the global conservation community is trying to understand the main factors determining diversity of species [2] and identifying important areas for their conservation [3], as this is crucial for their survival. This especially holds for threatened groups such as orchids [4, 5].

The orchid family is regarded as one of the largest and most diverse taxa of this rank in the flowering plant kingdom, with estimates of 880 genera and about 20,000–35,000 species [6–8]. Orchids are found in many different habitats but not in areas that are extremely cold or dry throughout the year [9]. Many characteristics, such as great species richness, its specific role in ecosystem, or endangered situation make it crucial to explore the distribution and conservation status of Orchidaceae [10]. It is an important group with respect to conservation biology [11] being at the frontline of extinction [12].

Species distribution models (SDMs) are a useful tool, which is now often applied in many branches of biogeography, conservation biology, and ecology [13], especially when threatened species are concerned [14]. These numerical tools combine species occurrence records with environmental data [13]. In combination with GIS techniques, these models are especially important and useful for predicting occurrence of rare species [15] especially in areas where certain parts are not fully explored. The species distribution models are then the only means enabling prediction of biodiversity for the group in question in such areas.

In our study, we used the maximum entropy algorithm in the MaxEnt application [16–19]. This algorithm uses maximum entropy and Bayesian methods to estimate the probability distribution of each species based on their presence or absence. Since becoming available in 2004, MaxEnt has been utilized extensively for modeling species distributions. This approach was used by conservation practitioners for predicting the distribution of a species from a set of occurrence records and environmental variables [19, 20] as well as in numerous other fields of biology and ecology that cover diverse aims across ecological, evolutionary, conservation, and biosecurity applications [19]. 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, for example, see [21–24]. Presence-only modeling methods require exclusively a set of known species occurrences together with predictor variables such as topographic, climatic, edaphic, biogeographic, and/or remotely sensed data [17, 18]. As an output from the MaxEnt program, we get extensive information, for example, maps of distribution of suitable niches and contribution of input variables to the model.

Here, we show an example of using the species distribution models for analyses of orchid species occurrence in the Czech Republic. We estimated which climatic, environmental, and other associated factors influence the distribution of two selected species and tried to find a new, yet unknown, localities in area selected. A similar approach was previously used in the study concerning conservation of orchid species in the Greek island of Crete [3].

2. Materials and methods

Our study site was located in the south of the Czech Republic (**Figure 1**). This area of South Bohemia with about 10,057 km² extends between 400 and 800 m above sea level and is known for many localities of different orchid species, including even critically endangered species in the Czech Republic, such as *Liparis loeselii* or *Malaxis monophyllos*. The advantage of this area is

in quite a small human population density, which allows preserving a natural environment suitable for endangered species.

As a source of data, we used information from 5 databases—the database of the Nature Conservation Agency of the Czech Republic [25], the Czech National Phytosociological Database, and the Floristic Documentation, both deposited at the Department of Botany and Zoology, Faculty of Science of the Masaryk University in Brno [26], the database of the South Bohemian Branch of the Czech Botanical Society [27] and the database of the inheritance of the late František Procházka (10,000 items, digitized from original cards). All data from these databases are deposited in one comprehensive database at the Global Change Research Institute (CAS), Department of Biodiversity Research in České Budějovice, but in order to protect the orchids in the localities, there is no public access to either of these databases.

During 2014–2016, we visited as many localities as possible to check, whether a selected orchid species is still present there or not. If the species was found, the number of flowering plants was counted and all important information, such as accurate GPS coordinates, how the locality looked like, or if it was mown or not was registered. The total of 428 localities was checked.

Because of special demands of methods in MaxEnt we used, only the two most numerous species were incorporated in all analyses. The first one was *Dactylorhiza majalis* (Rchb.) P.F. Hunt & Summerh., which lives in wet meadows, and the second species was *Platanthera bifolia* Rich., which flourishes in light deciduous forests.

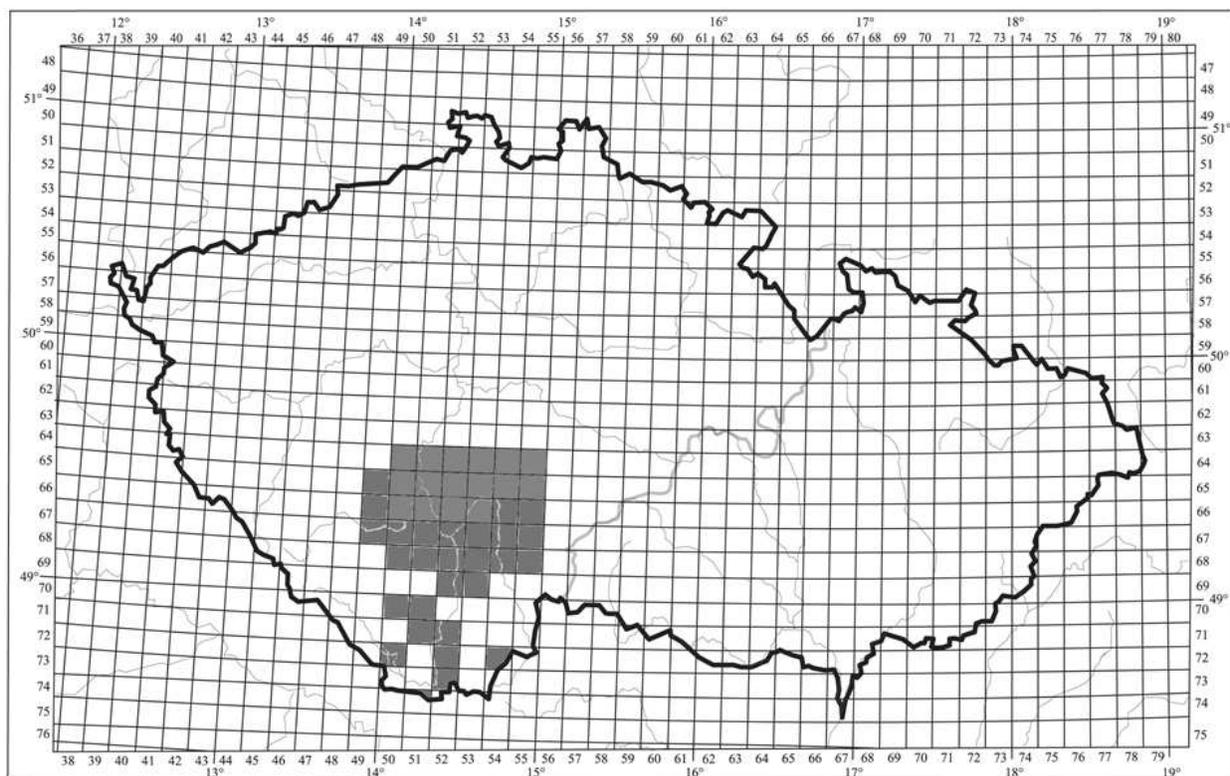


Figure 1. Map of the study site in the Czech Republic.

A set of environmental and habitat variables was prepared using available datasets for the Czech Republic. They were divided into two groups according to its spatial scale and ecological meaning (**Table 1**).

All analyses were conducted by the MaxEnt program version 3.3.2 [17–19]. In this program, we first performed the jackknife procedure, which told us how the species reacts to different environmental factors. Two different blue bars are always displayed in the resulting figure. The length of the dark-blue bar tells us, how large the impact of the selected factor is. The length of the light-blue bar tells us, how much information would be lost, if the corresponding factor were excluded from the analysis. Thus, deletion of a factor associated with the long light-blue bar would cause a large loss of explanatory power of the model. Then we performed three analyses for each species.

Before describing these, we have to elucidate the meaning of one factor used in the analyses that consists of 40 subfactors: the meaning of the “consolidated layer of ecosystems” (KVES) [28].

	<i>Dactylorhiza majalis</i>	<i>Platanthera bifolia</i>
Analysis 1	dem frost_days precipitation solar_rad summer_days trop_days veg_season temp_1 temp_2 KVES slope	dem frost_days precipitation solar_rad summer_days trop_days veg_season temp_1 temp_2 KVES slope
Analysis 2	KVES_4 KVES_5 KVES_6 KVES_20 KVES_21 KVES_39 KVES_maj KVES_var orna_p_buff TPI veg_sez vert_het zapl_pl	KVES_4 KVES_5 KVES_6 KVES_20 KVES_21 KVES_39 KVES_maj KVES_var orna_p_buff TPI veg_sez vert_het zapl_pl
Analysis 3	alkali KVES KVES_4 KVES_6 KVES_var op_buff reactivity	alkali KVES KVES_5 KVES_var op_buff reactivity solar_rad vert_het

Table 1. Description of variables used in the analyses.

KVES is a list of 40 types of habitat type, named as KVES_1, KVES_2, ..., KVES_40. For example, KVES_4 means alluvial and wet meadows, KVES_5 means dry grasslands, and so on (see **Table 2** for further examples). According to our knowledge, encompassing many years of orchid research, and to the information published in literature on ecological requirements of individual

Code	Description
Alkali	Alkalinity of rocks in a bedrock
dem	Altitude
frost_days	Number of freezing days per year
KVES	consolidated layer of ecosystems
• 4	• Alluvial and wet meadows
• 5	• Dry grasslands
• 6	• Mesophilic meadows
• 10	• Oak and oak-hornbeam forests
• 12	• Beech forests
• 13	• Dry pine groves
• 17	• Natural shrubs
• 18	• Vegetation of standing waters
• 19	• Wetlands and coastal vegetation
• 20	• Peat bogs and water springs
• 21	• Rocks and brushes
• 23	• Swamps and marshes
• 30	• Mixed forests
• 33	• Urban green areas, gardens, parks, or cemeteries
• 34	• Sports and recreational areas
• 39	• Agricultural meadows
• maj	• Dominant habitat type
• var	• Habitat heterogeneity (amount of different types of habitats)
orna_p_buff	Amount of arable land in the square of 500 to 500 m (%)
op_buff	Amount of arable land in the buffer zone of 250 m from particular orchid species (%)
precipitation	Total precipitation per year (mm)
reactivity	Reactivity of rocks in a bedrock
slope	Slope of terrain (°)
solar_rad	Solar radiation—total amount of incoming solar insolation (WH/m ²)
summer_days	Number of summer days (with temperature exceeding 25°C) per year
temp_1	Mean yearly temperature (°C)
temp_2	Temperature variability during year (°C)
TPI	Topographic position index
trop_days	Number of tropical days (with temperature exceeding 30°C) per year
veg_season; veg_sez	Duration of vegetation season
vert_het	Vertical heterogeneity (standard deviation of altitude)
zapl_pl	Periodically flooded areas (binary variable)

Table 2. Description of all important factors used in all analyses.

orchid species [29–32], we suspected that these factors might be important for determination of the occurrence of these species and therefore we included them into the analyses. KVES without a number means the presence of the certain habitat class, therefore it is a categorical variable. If this proves to be statistically significant, it means that the occurrence of the corresponding orchid species depends on some habitat type. Sometimes also the environmental heterogeneity (here called KVES_var—see **Table 2**), expressed as the number of different KVES types per unit area (sometimes also called “grain size” in the literature, especially in the landscape ecology jargon) may be important—large KVES_var means that the landscape consists of a mosaic of many small units like fields, pastures, meadows, forests, and so on, which usually indicates low-intensity agriculture and subsequently a likely good habitat for protected species. Therefore, the KVES_var is sometimes included in our analyses. Similarly, variable KVES_maj provides information about dominant habitat type within the assessed zone.

The KVES variable was used in Analysis 1, as described later. For any orchid species, particular vegetation types might be characteristic—for example, KVES_4 (alluvial and wet meadows) may—according to our knowledge—characterize a typical habitat for *Dactylorhiza majalis*. Thus, in subsequent analyses, only those vegetation types, which we suspected as candidates for description of the presence of the corresponding orchid species, were selected, as described in **Table 1**. Detailed description of the particular KVES values is given in **Table 2** only for those KVES factors used in the analyses. So, the three analyses were as follows.

In Analysis 1, the influence of climatic variables and other basic abiotic gradients on orchid distribution was studied. The list of these factors is shown in **Table 1** and their description in **Table 2**. The climatic data were obtained from the Global Change Research Institute of the CAS and a climate character from a timeline of 1981–2011 was created. Besides of the climatic factors, we also added KVES and slope of the terrain [33] as additional factors that could influence the distribution of *Dactylorhiza majalis* and *Platanthera bifolia*. This analysis was aimed to test, to which extent climate may affect the occurrence of the studied orchid species. However, at least some of other most important environmental nonclimatic factors had to be included, too, in order not to indulge into a purely climatic model, which does not seem to be appropriate in our case—our knowledge and literature information tells us that climate itself is not able to fully explain presence of orchid species in these temperate and rather flat regions [29–32]. There was no risk in including these additional factors—if our expectation did not come true, then these factors would just prove to be not significant.

As the results of Analysis 1 were not describing the presence of the studied species sufficiently in either of the studied species, we performed Analysis 2, which was more specific to selected environmental variables—particular KVES values. We selected these according to our experience and to the indications given in orchid literature—description of ecological requirements of the studied orchid species [29–32]. We also added the topographic position index (TPI), information about periodical floods (zapl_pl), and the amount of arable land in the square of 500 to 500 m (orna_p_buff) and similarly the amount of arable land in the buffer zone of 250 m from particular orchid species (op_buff), duration of vegetation season (veg_sez), and vertical heterogeneity (vert_het; see **Table 1**) as they might be important for the occurrence of particular orchid species. TPI classifies the landscape into slope position and landform category and

tells us at which position the locality is in the terrain—for example, whether it is on the top of a hill, in a valley, or near a depression. The information about periodical floods (zapl_pl) help us to determine whether the studied species prefer dry or wet areas or whether the probability of occurrence is higher in wet or dry localities. Another important factor influencing the occurrence of orchid species is the amount of arable land near the selected locality (orna_p_buff and op_buff). These two similar factors have a great impact on the distribution of orchids because with the increasing amount of arable field in the vicinity of localities, the probability of occurrence of studied species decreases rapidly, almost to zero. Arable lands are highly influenced by humans and full of artificial nutrients that are not suitable for the occurrence of orchids in general. The duration of vegetation season (veg_sez) was also added into this analysis but it has no important influence on the distribution of the studied species because the length of the vegetation season does not differ across the whole country. The last important environmental variable is vertical heterogeneity (vert_het). This factor explains how much rolling is the landscape near the selected locality, so how many of different altitudes comprises the area. All of these factors are also explained in **Table 2**.

The final analysis, Analysis 3, then uses only those factors, which proved to contribute to the determination of the presence of the orchid species studied, which followed from the previous two analyses. These factors were selected as the most significant ones from the first and second analyses and their linking into one analysis should determine which of them has the highest impact on the occurrence of studied species in the selected area (see **Table 1**). It could be just one, as well as a combination of more of them. The influence of alkalinity and reactivity of rocks in bedrock of a particular locality was added into this analysis [34] because according to literature, particular orchid species prefer only one or two rock types [29, 30, 32]. The final potential distribution map was then created based on this analysis.

The detailed description of all factors used in each of these analyses is shown in **Table 1** and the description of each important factor used in all analyses is shown in **Table 2**.

3. Results and discussion

3.1. *Dactylorhiza majalis* (Rchb.) P.F.Hunt & Summerh

3.1.1. Analysis 1: climatic factors

The jackknife procedure in **Figure 2** indicates that many of the variables included in this analysis have a certain impact on this species. However, in Central Europe, because of the rather flat terrain, the mesoclimatic variables reflect the position in a particular region (such as South Bohemia, or Northern Moravia or so) rather than exact position of the point considered. In other words, the same set of mesoclimatic conditions characterizes a relatively large area, rather than a particular point. Therefore, the set of mesoclimatic variables found in the localities was characteristic for South Bohemia rather than for occurrence of orchids. For example, in **Figure 3**, there is not a clear trend, as the values are only precipitation values in the particular localities. Therefore, neither precipitation, nor other mesoclimatic variables were used for the

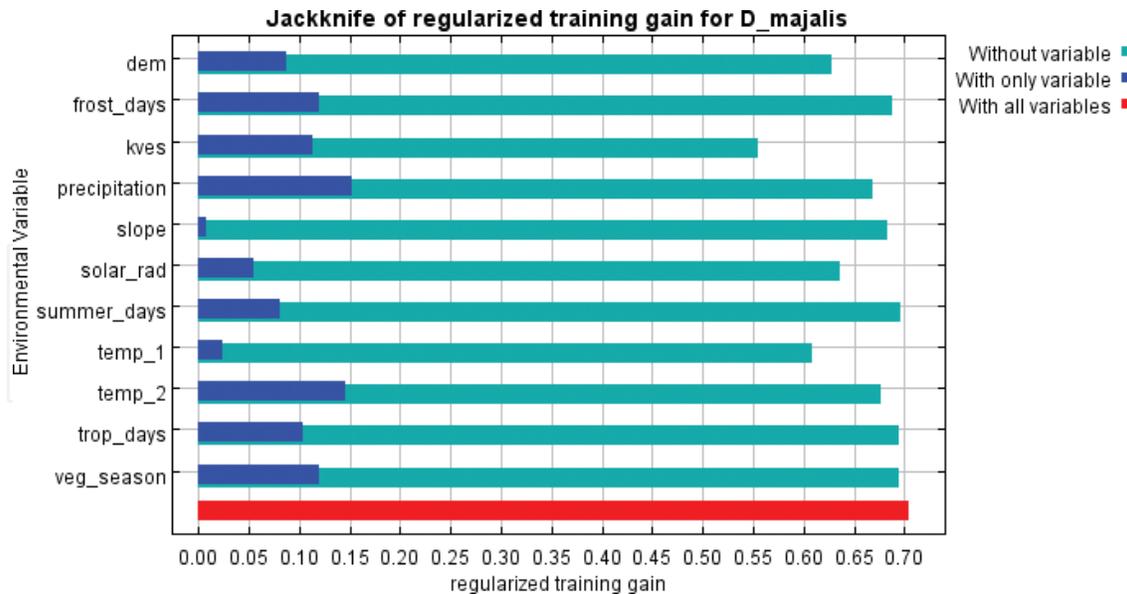


Figure 2. Graph of the jackknife procedure of climatic factors for *Dactylorhiza majalis*.

final analysis, even if their impact (especially that of precipitation) was high according to Figure 2. The only factor used for the final Analysis 3 was KVES.

3.1.2. Analysis 2: environmental factors of biotope and surroundings

Figure 4 shows the effect of various factors examined to the distribution of *D. majalis*, according to this analysis. Clearly, KVES_6 (mesophilic meadows) is the most important (the corresponding dark-blue bar is long). Also KVES_var (habitat heterogeneity) and orna_p_buff (amount of arable land in the square of 500 to 500 m) are important.

A closer look at pictures of environmental variables that had a significant effect on the distribution of *D. majalis* (Figure 5) reveals certain patterns:

- Figure 5A indicates the impact of mesophilic meadows (KVES_6) on the distribution of this species. It is clearly visible that the more mesophilic meadows are present, the bigger likelihood of occurrence of the studied species.
- Figure 5B shows that *D. majalis* prefers landscape consisting of a mosaic of many smaller biotopes. This confirms our expectation that this species is more likely to occur in such landscapes, probably because they are characteristic for low-intensity agriculture.
- Figure 5C shows that *D. majalis* is less likely to occur in landscapes with a large proportion of arable land. This is in accord with the published literature, which confirms that *Dactylorhiza majalis* is sensitive to any kind of eutrophication from arable fields that contain artificial fertilizers full of nitrogen and phosphorus [29–32]. These fertilizers are the cause of extinction of some localities because the more arable land is present around a suitable locality, the lower is the probability of occurrence of this species.
- Figure 5D shows the dependence of the likelihood of presence of *D. majalis* to various subfactors of KVES. The most suitable biotopes indicated by this figure are alluvial and

wet meadows (KVES_4), mesophilic meadows (KVES_6), in vegetation of standing waters (KVES_18), and wetlands and coastal vegetation (KVES_19). All these biotopes are wet, which is in agreement with ecological demands of this species [30–32]. According to our analysis, this species can also occur in urban green areas, gardens, parks, or cemeteries (KVES_33), which was confirmed by our personal observation, and then in agricultural meadows (KVES_39) that could become beneficial for orchid occurrence, if a suitable

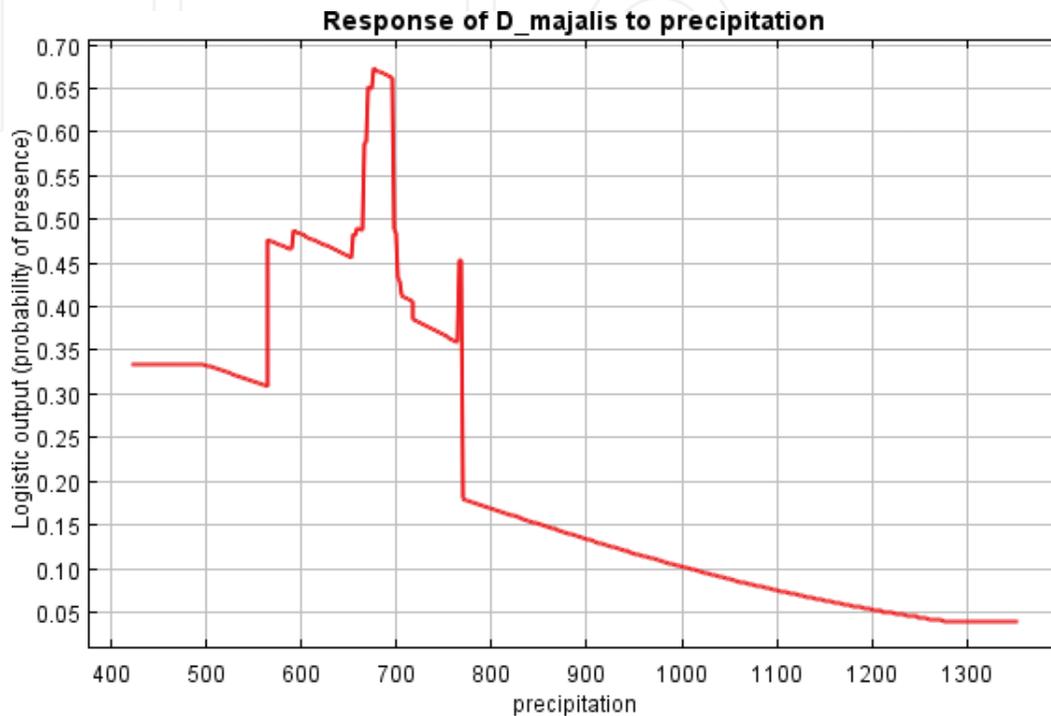


Figure 3. Response of *Dactylorhiza majalis* to precipitation.

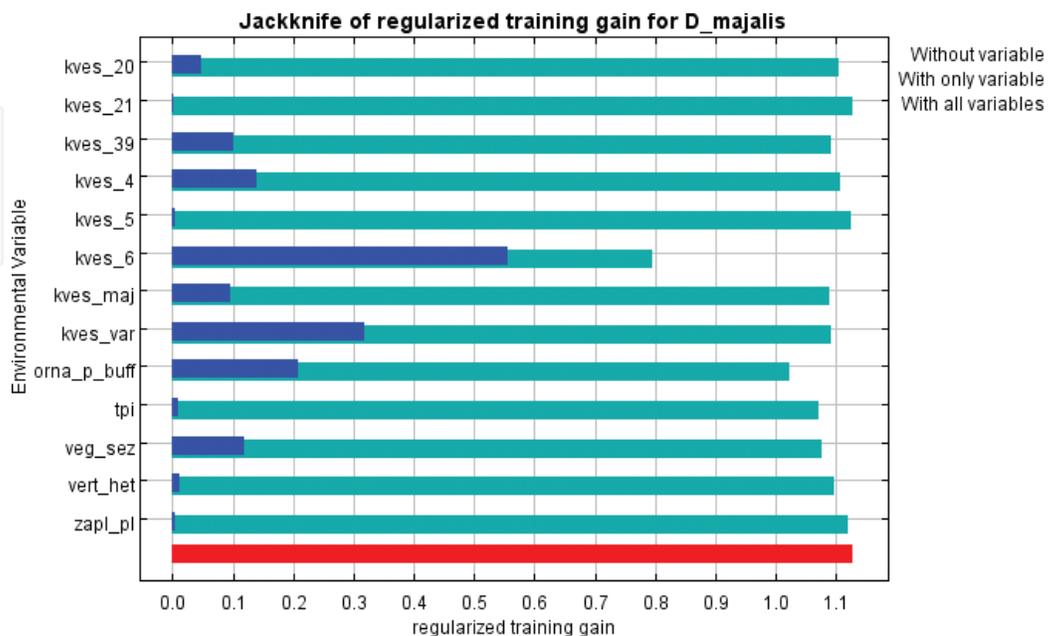


Figure 4. Graph of the jackknife procedure of environmental factors for *Dactylorhiza majalis*.

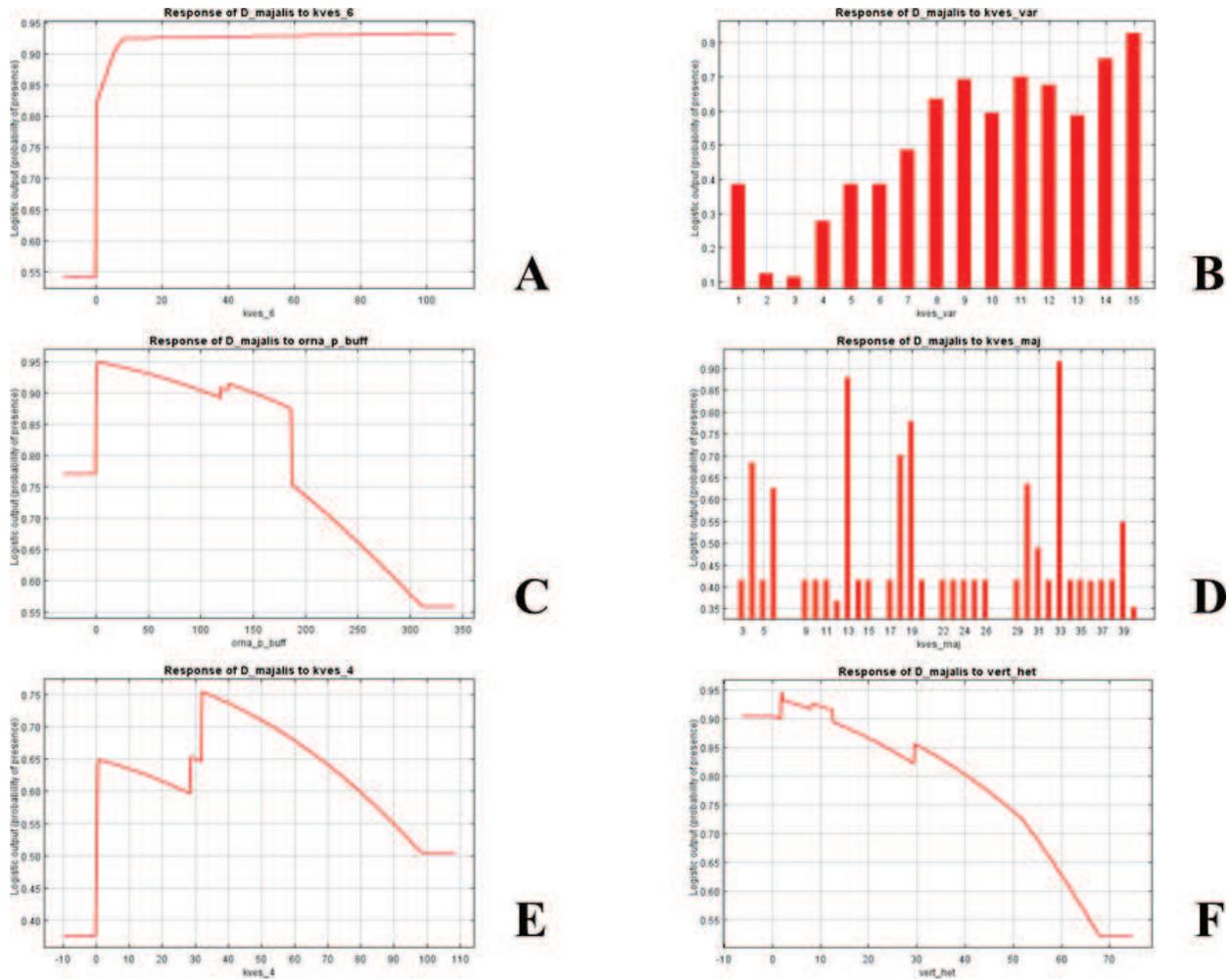


Figure 5. Response of *Dactylorhiza majalis* to: (A) presence of mesophilic meadows around the locality (KVES_6), (B) habitat heterogeneity (KVES_var), (C) cover of arable land around the locality (orna_p_buff); (D) consolidated layer of ecosystems (KVES), (E) presence of alluvial and wet meadows around the locality (KVES_4), and (F) vertical heterogeneity (vert_het).

management is applied. We can also see some inconsistencies in occurrence of *D. majalis*: its occurrence in dry pine groves (KVES_13) and mixed forests (KVES_30). Dry pine groves are not a suitable habitat for this species; this strange result could have been caused by border zone of two different habitat types. In mixed forests, a clearing could be a possible habitat.

- **Figure 5E** shows the dependence of the probability of occurrence of *D. majalis* on the presence of alluvial and wet meadows around the locality. The curve in the graph implies that there is a larger probability of occurrence of this species in areas with at least some of these types of habitats. We expected that there will be bigger dependence on wet meadows, but our data did not confirm this, which is interesting. We assume this might have been caused by human impact, because the studied area lies outside of larger protected areas. Wet meadows are not suitable for agriculture, because agricultural machinery is not able to work here and some of such meadows were extensively changed

and dried. Because of this, some of the existing localities are in the vicinity of wet meadows and some are not. But still we can see a trend that higher occurrence of *D. majalis* is in the vicinity of alluvial and wet meadows, and therefore use this factor in the final Analysis 3.

- **Figure 5F** shows the impact of vertical heterogeneity on the occurrence of *D. majalis*. According to this graph, this species occurs more in flat areas without stronger ripple of terrain. This is not surprising, because it is a meadow species. This factor was not used in the final analysis, however, because the dependence found was not strong.

3.1.3. Analysis 3: final analysis of the most important factors from the two previous analyses

This final analysis was prepared on the basis of the most important factors, which were determined from the previous analyses mentioned above. These factors are KVES_6 (presence of mesophilic meadows around the locality), KVES_4 (presence of alluvial and wet meadows around the locality), KVES (consolidated layer of ecosystems) in general, op_buff (cover of arable land in the buffer zone of 250 m from particular orchid species), and KVES_var (habitat heterogeneity). Alkalinity and reactivity of rocks in the bedrock near the selected locality were also added into this analysis. The resolution of the final potential distribution map (**Figure 6**) was set to a square grid of 50 × 50 m to make the map more precise and detailed for determining possible new localities with suitable conditions for *D. majalis*. This map shows there are other suitable localities for potential occurrence of the studied species in the region of South Bohemia; they are located in the surroundings of cities of Vyšší Brod, Jistebnice, Blatná, and Stachy. Suitable places are also around the Šumava National park and to the east of Kunžak city and the city of Jindřichův Hradec. This distribution map can help us to find new, yet unknown localities of *D. majalis* and be useful for conservation strategies of this endangered species in the Czech Republic.

Figure 7 shows the effect of the most important factors examined to the distribution of *D. majalis*. The responses of the species to selected factors are quite high, so we were right with the selection of environmental factors. Clearly, the most important factor is KVES (consolidated layer of ecosystems). Other important factors are also KVES_6 (presence of mesophilic meadows around the locality) and KVES_var (habitat heterogeneity). According to this analysis, alkalinity and reactivity of rocks, the newly added factors, have the lowest impact on occurrence of *D. majalis*. It is caused by broad ecological demands of this species to pH conditions in the soil [29–32].

A closer look at pictures of the most important variables that had a significant effect on the distribution of *D. majalis* (**Figure 8**) reveals some interesting patterns:

- **Figure 8A** shows the dependence of the likelihood of presence of *D. majalis* to various subfactors of KVES after the accuracy improvement of resolution. According to this figure, the most suitable biotopes for this species are alluvial and wet meadows (KVES_4), mesophilic meadows (KVES_6), wetlands and coastal vegetation (KVES_19), peat bogs and water springs (KVES_20), and green urban areas, gardens, or parks (KVES_33). The occurrence of this species was also recorded in natural shrubs (KVES_17), swamps and

marshes (KVES_23), and in sports and recreational areas (KVES_34). These types of biotopes could be also suitable for *D. majalis* because most of them are wet or somehow maintained, for example, by mowing (such as recreational areas or parks) and this species was really found in the field in these kinds of biotopes. Biotope of dry pine groves

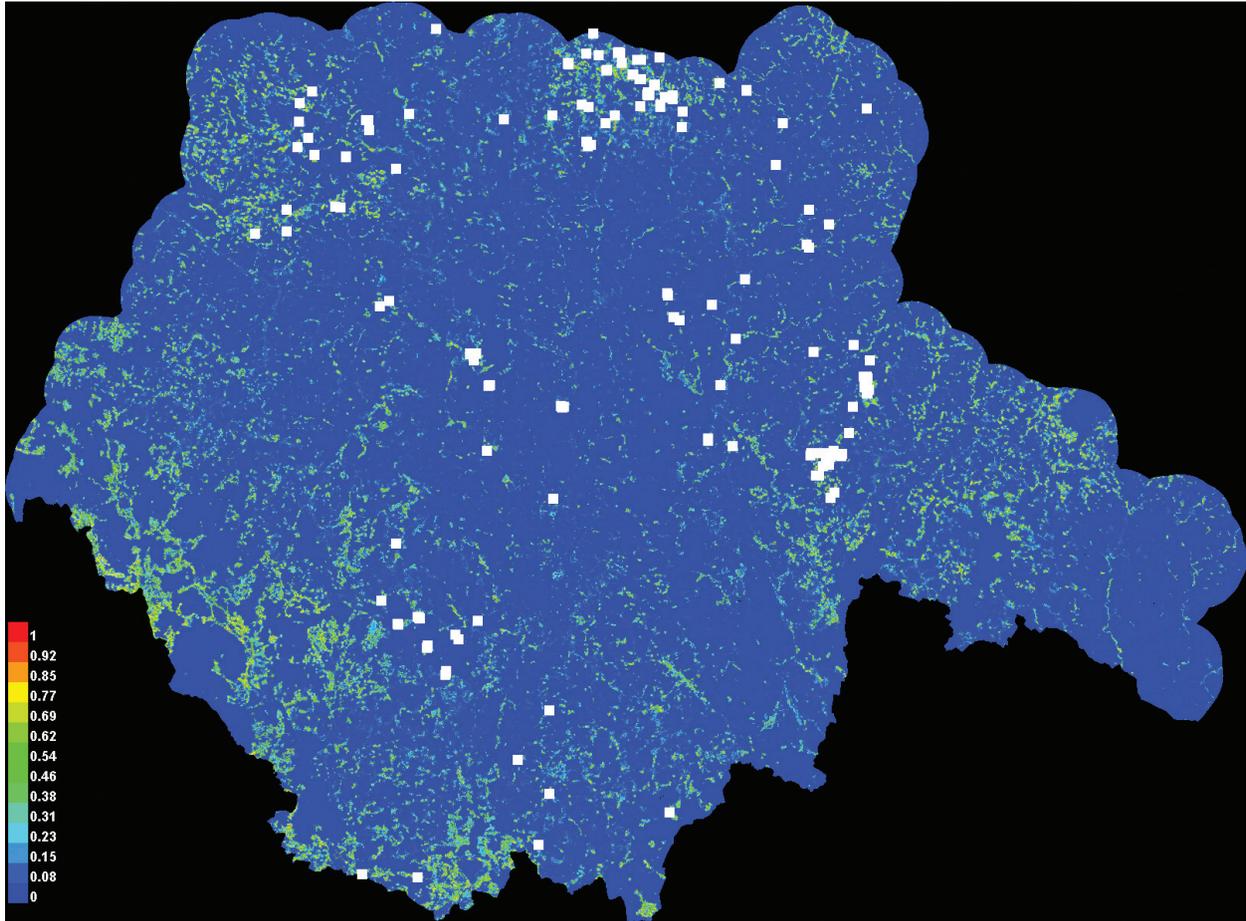


Figure 6. Potential distribution map of *Dactylorhiza majalis* in the region of South Bohemia.

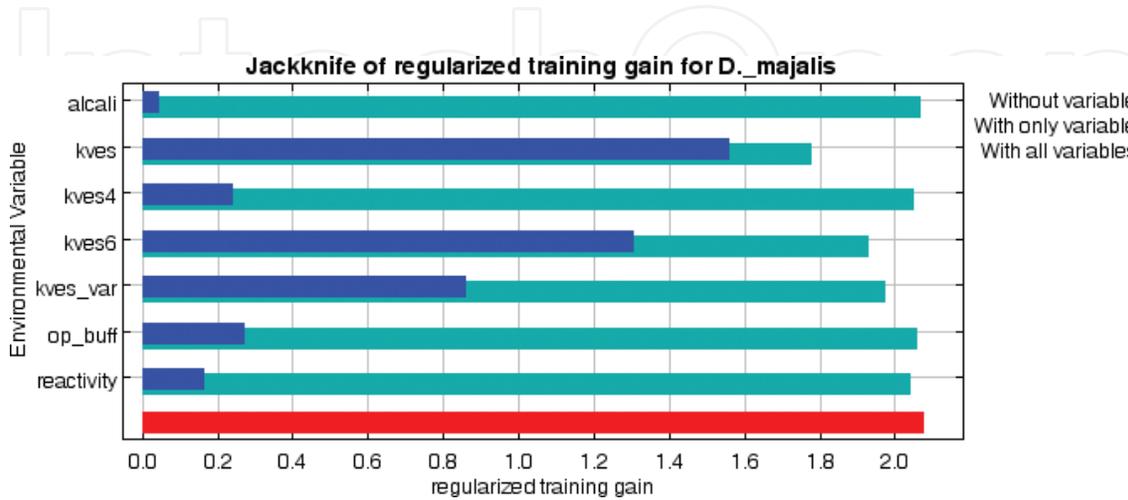


Figure 7. Graph of the final jackknife procedure of the most important factors for *Dactylorhiza majalis*.

(KVES_13) was correctly excluded from the analysis as an unsuitable biotope for the occurrence of *D. majalis* because of the accuracy improvement of resolution.

- **Figure 8B** shows another factor, which has an important impact on the occurrence of this species. It indicates that *D. majalis* prefers landscape consisting of a mosaic of many smaller biotopes, as was proved in the previous analysis. This confirms our expectation that this species could more likely be found in these types of landscapes, probably because they are not changed so much by the intensity of agriculture.
- **Figure 8C** shows the impact of alkalinity of rocks in bedrock of the locality on the occurrence of *D. majalis*. It is visible that this species occurs on many types of rocks from the point of view of their pH values and does not prefer any specific type of bedrock. However, its occurrence is more frequent on more acidic soils, probably because wet localities have usually lower pH values.
- **Figure 8D** shows the impact of mesophilic meadows (KVES_6) on the distribution of *D. majalis*. According to the final jackknife procedure (**Figure 7**), this factor had an important impact on the occurrence of studied species. **Figure 8D** indicates that this species is more likely to occur in areas in the vicinity of at least some part of this biotope. But there is no curve of growth or decline in the graph that could be clearly interpretable. So we could presume that *D. majalis* prefers an area where mesophilic meadows are present, because

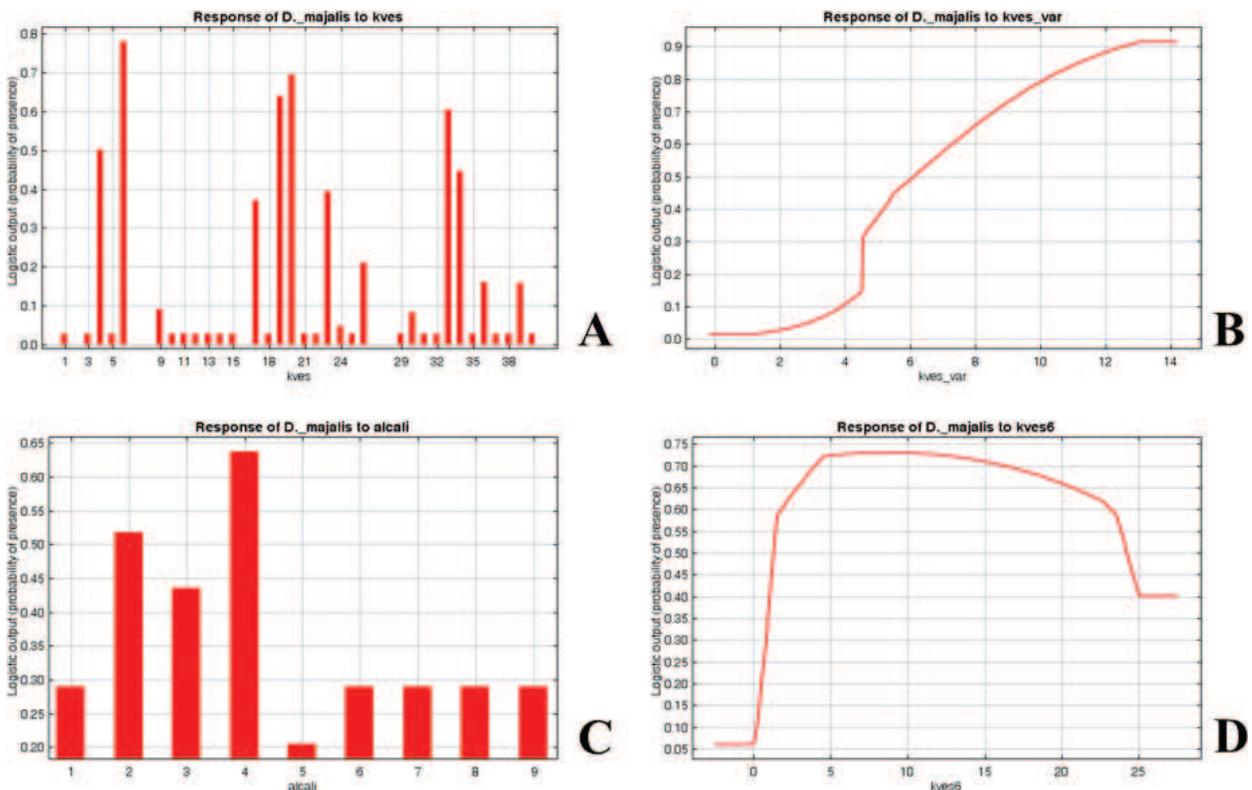


Figure 8. Response of *Dactylorhiza majalis* to: (A) consolidated layer of ecosystems (KVES), (B) habitat heterogeneity (KVES_var), (C) alkalinity of rocks in a bedrock (alkali), and (D) presence of mesophilic meadows around the locality (KVES_6).

these types of meadows are suitable for its occurrence [29, 30, 32]. However, an interpretation that the occurrence of *D. majalis* is strongly dependent on the presence of mesophilic meadows near the locality would be incorrect.

3.2. *Platanthera bifolia* (L.) Rich.

3.2.1. Analysis 1: climatic factors

The results of the jackknife procedure in **Figure 9** revealed that the consolidated layer of ecosystem (KVES) is the most important factor influencing the distribution of *Platanthera bifolia*. Other important factors are solar radiation (solar_rad) and slope of the terrain (slope). Again, we did not use the precipitation for further analyses because of reasons described earlier (in Analysis 1 for *Dactylorhiza majalis*).

A closer look at pictures of factors from Analysis 1 that had a significant effect on the distribution of *P. bifolia* (**Figure 10**) shows interesting results.

- **Figure 10A** indicates which type of biotope (KVES) this species prefers. It was found mostly in oak and oak-hornbeam forests (KVES_10), beech forests (KVES_12), and also in mixed forests (KVES_30). These results are in agreement with our knowledge and information from the literature [29, 30, 32], because this is a forest species and prefers similar types of deciduous forests.
- **Figure 10B** shows a response of the studied species to solar radiation (solar_rad), a typical mesoclimatic factor. In the Czech Republic, the extent of solar radiation is not different across the whole country so this factor tells us, whether *P. bifolia* prefers shadow or sunny places. From this graph, it is clearly visible that it is more likely to find this species in shady places. As it was said before, it is in accordance with information from literature [29–32].

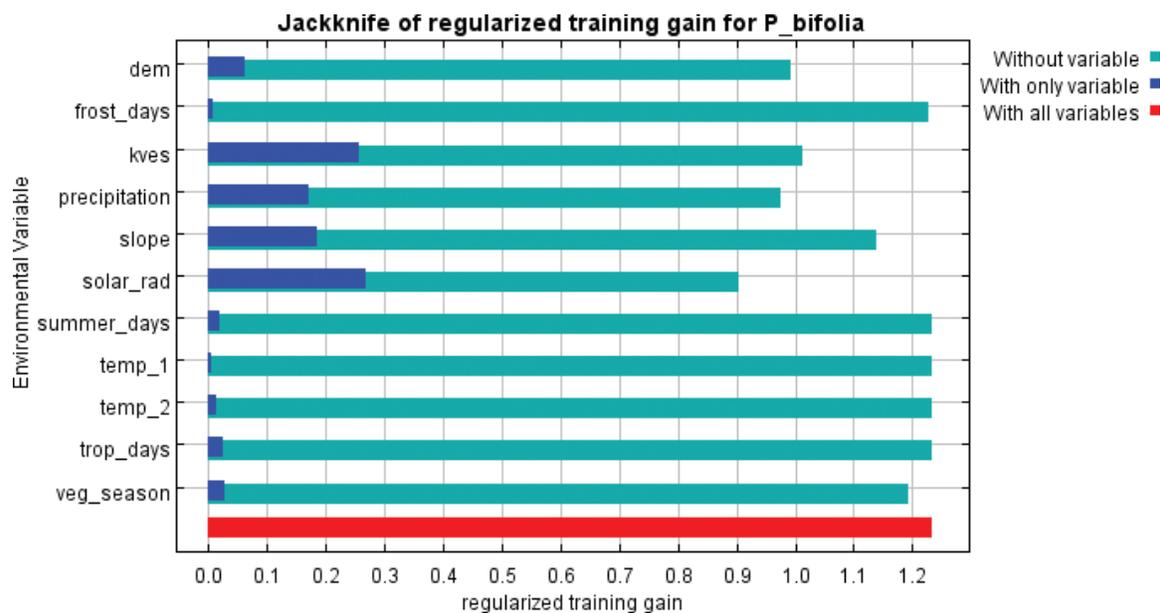


Figure 9. Graph of the jackknife procedure of climatic factors for *Platanthera bifolia*.

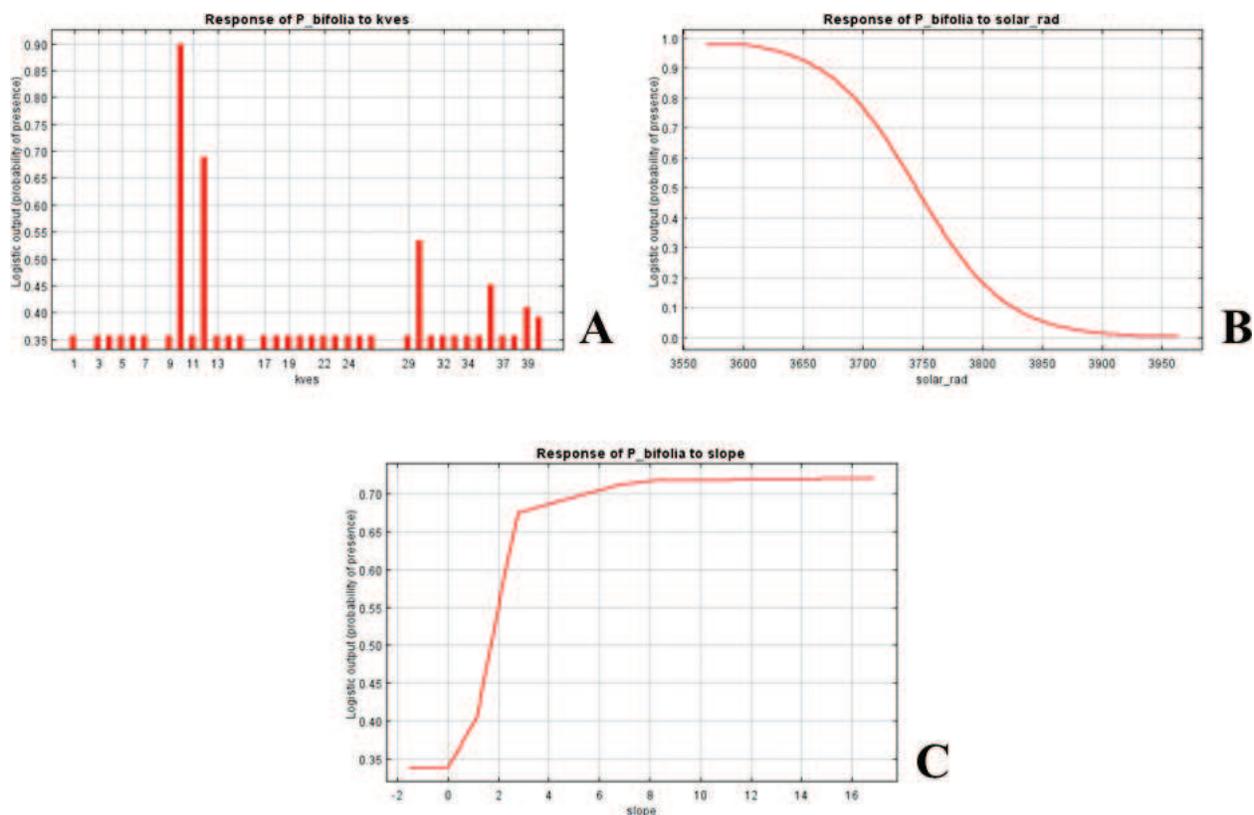


Figure 10. Response of *Platanthera bifolia* to: (A) consolidated layer of ecosystems (KVES), (B) solar radiation (solar_rad), and (C) slope of the terrain (slope).

- **Figure 10C** shows the impact of a slope of terrain on the occurrence of *P. bifolia*. According to this picture, there is a low possibility to find this species in a completely flat landscape. This means that it prefers a specific change of altitudes in given area.

3.2.2. Analysis 2: environmental factors of biotope and surroundings

Figure 11 shows the effect of various environmental factors examined on the distribution of *Platanthera bifolia*, according to this analysis. Clearly, the presence of dry grasslands (KVES_5) is the most important factor. Other important factors are habitat heterogeneity (KVES_var), vertical heterogeneity (vert_het), and the amount of arable land in the square of 500 × 500 m (orna_p_buff).

A closer look at the pictures of environmental variables that had a significant effect on the distribution of *Platanthera bifolia* (**Figure 12**) reveals certain patterns:

- **Figure 12A** shows the impact of vertical heterogeneity on the occurrence of studied species. This factor explains how much rolling is the landscape near the selected locality (amount of different altitudes). It is visible that there is almost zero probability of occurrence of this species in a flat landscape which means that *P. bifolia* prefers a heterogeneous landscape with hills and valleys. This is in accordance with the results of Analysis 1 of this species (**Figure 10C**), where the slope of terrain was one of the most important factors.

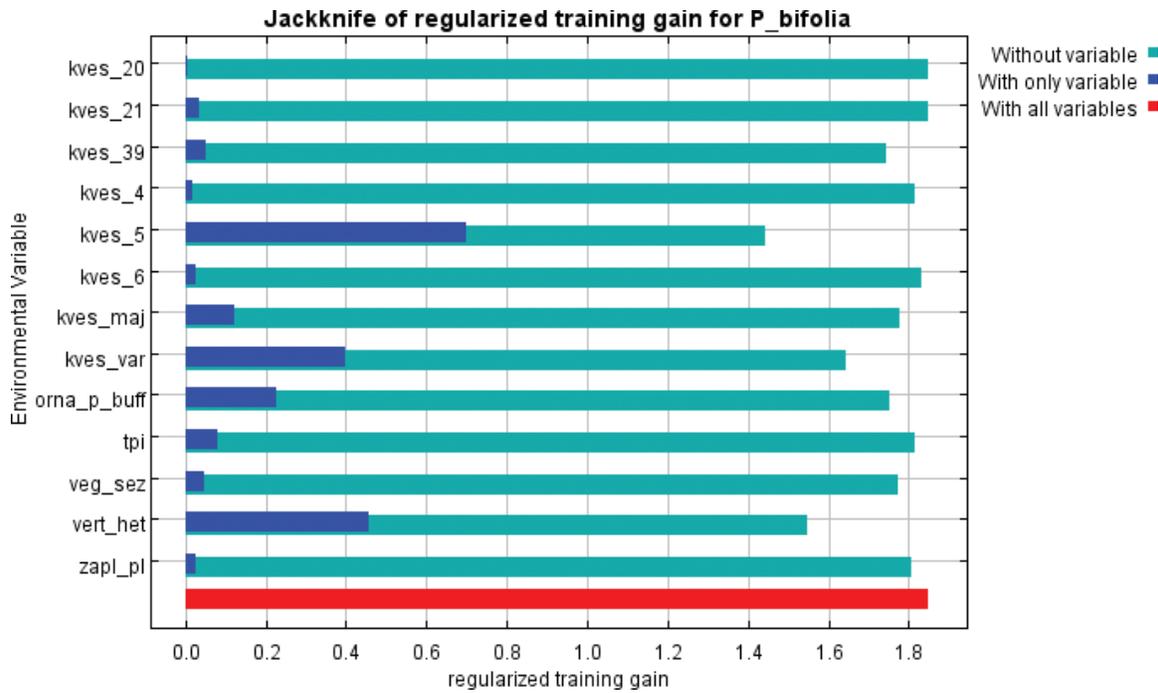


Figure 11. Graph of the jackknife procedure of environmental factors for *Platanthera bifolia*.

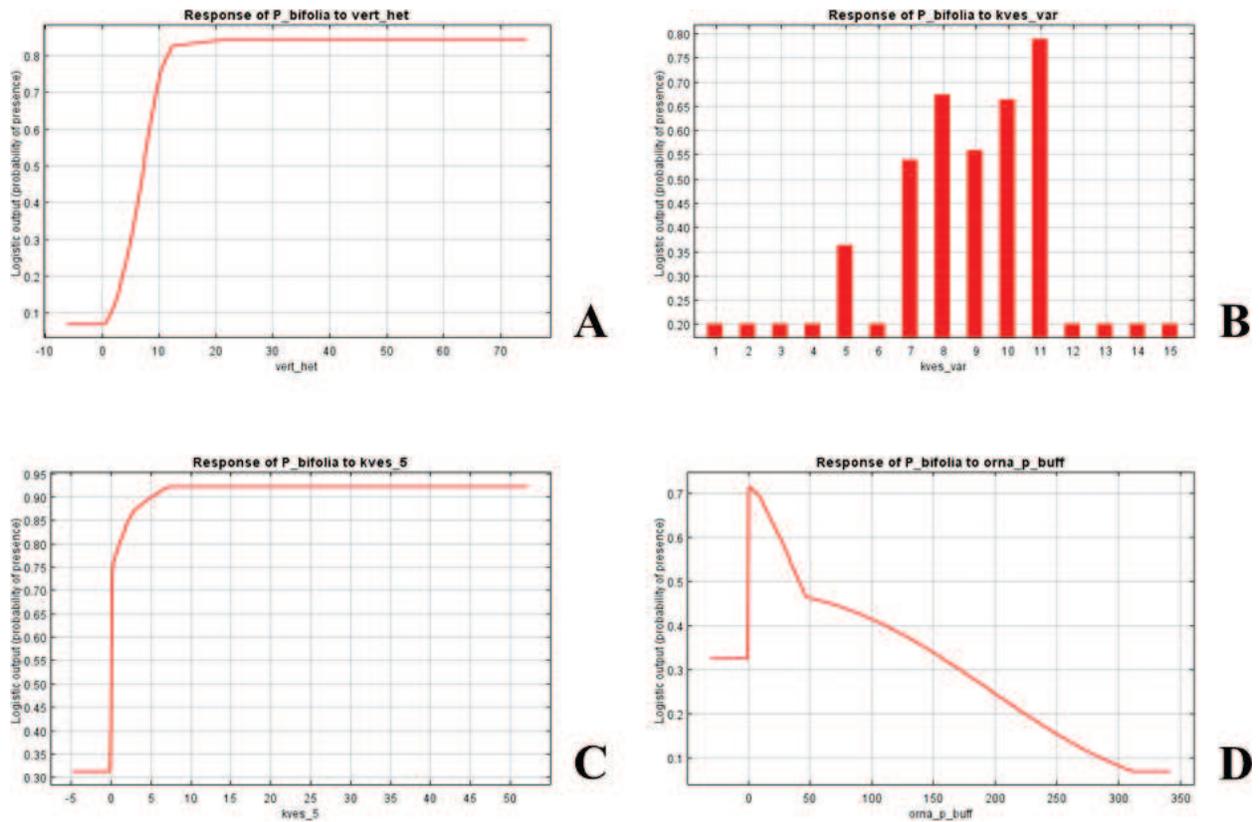


Figure 12. Response of *Platanthera bifolia* to: (A) vertical heterogeneity (vert_het), (B) habitat heterogeneity (KVES_var), (C) presence of dry grasslands (KVES_5), and (D) amount of arable land in the square of 500 to 500 m (orna_p_buff).

- **Figure 12B** shows the relationship between the presence of *P. bifolia* and habitat heterogeneity (KVES_var). Clearly, this species prefers areas with higher heterogeneity of the environment; it means areas which consist of many small habitats. The probability of presence of this species in an area made of only one single habitat is almost zero. An increasing amount of agricultural areas and arable lands make *P. bifolia* more and more endangered.
- The impact of a presence of dry grasslands (KVES_5) near the locality with *P. bifolia* is shown in **Figure 12C**. This species prefers areas, the surroundings of which consist of dry grasslands. We can imagine a suitable locality as small patches of forests surrounded mainly by grasslands. Clearly, this factor is related with the previous one, the environmental heterogeneity. This species does not occur in the cultural landscape, but it prefers heterogeneous environment made of meadows and small patches of forests.
- **Figure 12D** shows a relationship between the occurrence of the study species and amount of arable land. From this picture, it follows that *P. bifolia* favors an area without arable land in its surroundings. If there are some areas with arable fields, the probability of occurrence of studied species rapidly decreases to almost zero.

3.2.3. Analysis 3: final analysis of the most important factors from the two previous analyses

The choice of the most important factors influencing the occurrence of *Platanthera bifolia* was based on the results of the two previous analyses mentioned above. For the final analysis, consolidated layer of ecosystems (KVES), solar radiation (solar_rad), vertical heterogeneity (vert_het), habitat heterogeneity (KVES_var), amount of arable land in the buffer zone of 250 m from the corresponding orchid species site (op_buff), and the presence of dry grassland (KVES_5) were chosen as the most important factors. Alkalinity and reactivity of rocks in the bedrock were also added into this final analysis. The resolution of the final potential distribution map of *P. bifolia* (**Figure 13**) was again set to a square grid of 50 × 50 m to make the map more precise, as was the same case with the previous species. According to this map, there are still some places in the studied region that are suitable for a new occurrence of this species. The most suitable places for finding new localities are around the city of Sezimovo Ústí, Tábor, and Písek, then also to the south of Strakonice city and along the upper stretch of the Vltava River. This map could encourage orchid conservationists to find new, yet unknown, localities of this endangered species of the Czech flora.

Figure 14 shows responses of *P. bifolia* to the most important factors that influence its distribution in studied region. Clearly, the most important factors were consolidated layer of ecosystems (KVES), the presence of dry grasslands (KVES_5), the alkalinity of rocks in a bedrock (alkali), and vertical heterogeneity (vert_het). But all of factors that were chosen for final analysis had an interesting impact on the occurrence of this species.

A closer look at the picture of all factors used in Analysis 3 (**Figure 15**) revealed some important information about the influence of individual factors on the distribution of *P. bifolia*:

- **Figure 15A** shows the dependence of the likelihood of the distribution of *P. bifolia* on various subfactors of KVES. Clearly, the highest occurrence of this species was in dry

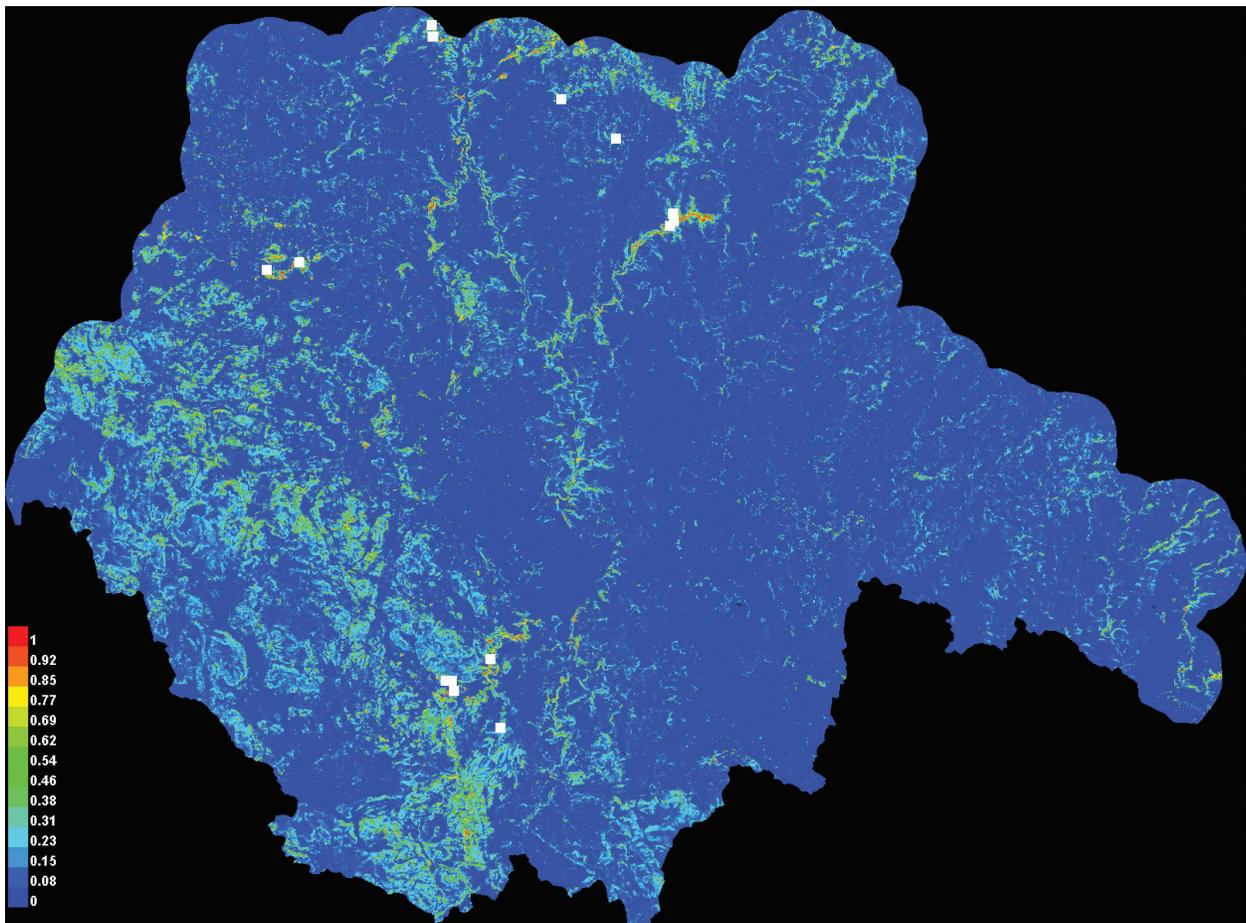


Figure 13. Potential distribution map of *Platanthera bifolia* in the region of South Bohemia.

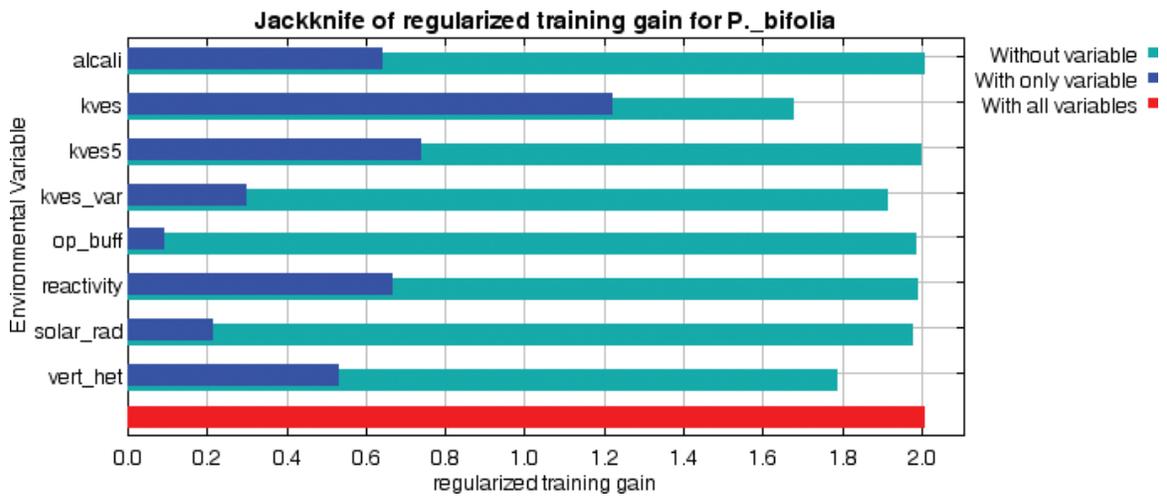


Figure 14. Graph of the final jackknife procedure of the most important factors influencing the occurrence of *Platanthera bifolia*.

grasslands (KVES_5) and in oak and oak-hornbeam forests (KVES_10). This species has a broad ecological valence and occurs both in forest and meadow biotopes that are poor in nutrients [29–31]. Because of this, all depicted biotopes in the picture that have a higher probability of presence than 0.3 are suitable for presence of *P. bifolia*.

- In **Figure 15B**, the impact of dry grasslands (KVES_5) on the occurrence of *P. bifolia* is depicted. It is clearly visible that with higher amount of grasslands near the selected locality, there is also a higher probability of the occurrence of the studied species. It means that this species prefers an area where grasslands are the dominating biotope in the surrounding of the selected locality. We can assume that this kind of biotope is preferable for *P. bifolia* because it is not managed intensively by humans and therefore no damage to suitable places by eutrophication or agricultural activities happens.

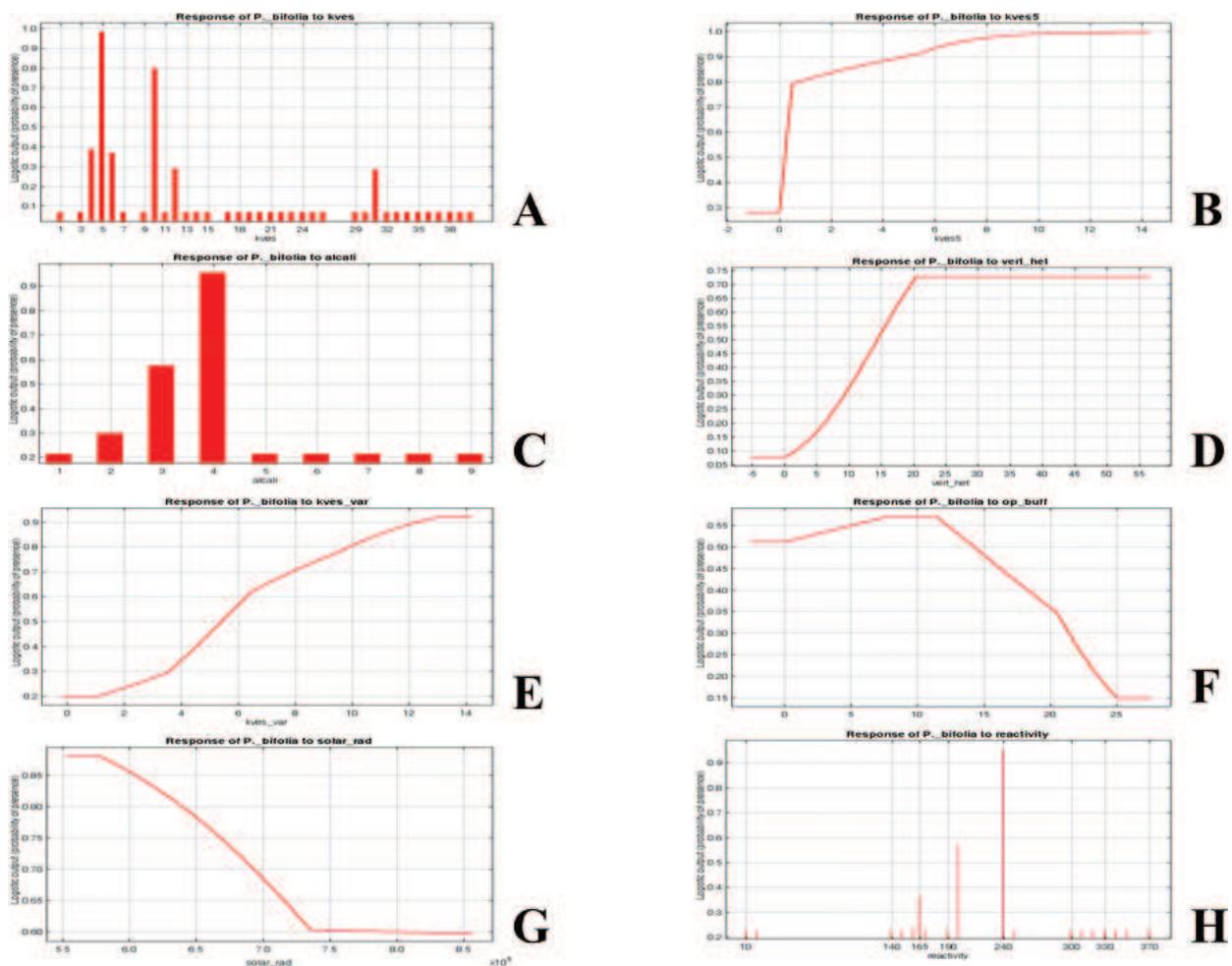


Figure 15. Response of *Platanthera bifolia* to: (A) consolidated layer of ecosystems (KVES), (B) presence of dry grasslands (KVES_5), (C) alkalinity of rocks in a bedrock (alcali), (D) vertical heterogeneity (vert_het), (E) habitat heterogeneity (KVES_var), (F) amount of arable land in the buffer zone of 250 m from particular orchid species (op_buff), (G) solar radiation (solar_rad), and (H) reactivity of rocks in a bedrock (reactivity).

- **Figure 15C** indicates the dependence of the occurrence of the studied species on the alkalinity of rocks in the vicinity of a locality (alkali). According to literature information, this species favors slightly acidic, as well as alkaline soils [30–32]. Clearly, this species mostly occurred in the soil type number 4 and prefers soils with high index of alkalinity—between 0.25 and 0.4 mol/kg. This index is a ratio of different amounts of components in a rock and corresponds to alkaline soils [34].
- **Figure 15D** shows the impact of vertical heterogeneity (vert_het) on the probability of occurrence of *P. bifolia*. It is obvious that the probability of occurrence of the studied species increases with increasing level of vertical heterogeneity, so the species prefers areas with different altitudes, as opposed to flat areas.
- In **Figure 15E**, the influence of habitat heterogeneity (KVES_var) on the distribution of studied species is shown. The impact of this factor does not differ from the impact in the previous analysis—the species favors a higher heterogeneity of the environment and a landscape structure with many different biotopes.
- **Figure 15F** indicates the impact of amount of arable land in the buffer zone of 250 m from particular orchid species (op_buff) on the distribution of the studied species. As in the previous analysis, this species occurs more probably in the area with a low amount of arable land in a buffer zone of 250 m around the selected locality. The reason of this dependence was explained above. Out of all important factors from the Analysis 3, this factor has the smallest impact on species occurrence.
- **Figure 15G** shows the dependence of species distribution on the amount of solar radiation (solar_rad). As it was said above, this species prefers shady places mainly in forests or bushes, which are typical habitats of *P. bifolia*.
- In **Figure 15H**, the impact of reactivity of rocks in bedrock near the locality (reactivity) on the occurrence of *P. bifolia* is depicted. Clearly, the studied species occurs on rocks of type number 240 and 200. These numbers correspond to metamorphic rocks with high amount of alkalinity such as dolerite, soapstone, or metagabro.

4. Conclusions

The Maxent program is a useful tool for predicting potential distribution of species, not only for orchids. Based on the results of this study, the most important factors for both studied species were types of vegetation cover of land (consolidated layer of ecosystems; KVES), the amount of arable land in the buffer zone of 250 m from particular orchid species (op_buff), and habitat heterogeneity (KVES_var).

Our results are very important and helpful in determination of new, yet unknown, localities of *Dactylorhiza majalis* and *Platanthera bifolia*, the endangered species of the flora of the Czech Republic. Without potential distribution maps, targeted searching of new localities, it would be only a random choice of orchid hunters. These results will help people interested in orchid

flora and their conservation to focus only on certain areas with the highest probability of occurrence of the selected species.

Basically, this work should serve as tool for better conservation of orchids and clear the way for understanding of important factors determining their distribution in the Czech Republic.

Acknowledgements

This work was supported by the Ministry of Education, Youth, and Sports of the CR within the National Sustainability Program I (NPU I), grant number LO1415.

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