Global Ecology and Conservation 47 (2023) e02642

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

North-facing roadside slopes: Anthropogenic climate microrefugia for orchids

Réka Fekete [a,b,c,*,1], Orsolya Vincze [d,e,2], Jenő Nagy [a,b,3], Viktor Löki [d], Kristóf Süveges [a], Judit Bódis [f], Tamás Malkócs [g,4], Ádám Lovas-kiss [d], Attila Molnár V. [a,b]

[a] Department of Botany, University of Debrecen, Egyetem sq. 1., H-4032 Debrecen, Hungary
[b] HUN-REN-UD Conservation Biology Research Group, Egyetem sq. 1, H-4032 Debrecen, Hungary
[c] Seed Ecology Research Group, Institute of Ecology and Botany, Centre for Ecological Research, 2-4 Alkotmány street, Vácrátót H-2163, Hungary
[d] Wetland Ecology Research Group, Department of Tisza Research, Institute of Aquatic Ecology, Centre for Ecological Research, Hungarian Research Network (HUN-REN), Bem sq. 18/C., H-4026 Debrecen, Hungary
[e] Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Clinicilor Street 5-7, RO-400006 Cluj Napoca, Romania
[f] Department of Conservation Biology, Institute for Wildlife Management and Nature Conservation, Georgikon Campus, Hungarian University of Agriculture and Life Sciences, Deák St. 16., H-8360 Keszthely, Hungary
[g] Department of Tisza Research, Centre for Ecological Research-DRI, Bem sq. 18/C., H-4026 Debrecen, Hungary

A R T I C L E I N F O

Keywords:
Orchids
Roadside
Climate change
Microclimate, microrefugia, anthropogenic habitat

A B S T R A C T

Facing global climate change is a great challenge for organisms. Numerous species respond to a changing climate by shifting their geographical ranges, adapting to the local climate or finding microrefugia to persist under unfavorable macroclimatic conditions. Orchids are frequently found in roadside verges, and it was demonstrated that roadsides could serve as refugia for them in a changing landscape. We investigated whether roadside slopes, facing different compass directions could serve as microrefugia for orchids, using our database spanning across 18 European countries. Our results showed that the probability of orchid occurrence in north-facing roadside slopes are greater than on south-facing slopes. Further, we found a significant difference in the probability of orchid occurrence in different exposures under unfavorable macroclimatic conditions. In south-facing slopes, the probability of orchid occurrence decreased with increasing annual mean temperature and increasing precipitation seasonality. This suggests that harsh microclimatic environments intensify the negative effects of the macroclimate in south-facing slopes. Moreover, roadside slopes with cooler microclimatic conditions might facilitate the persistence of orchids under a warming and increasingly stochastic climate.

* Corresponding author at: Department of Botany, University of Debrecen, Egyetem tér 1, H-4032 Debrecen, Hungary.
E-mail address: feketereka722@gmail.com (R. Fekete).
[1] ORCID ID: 0000-0002-9255-0012
[2] ORCID ID: 0000-0001-5789-2124
[3] ORCID ID: 0000-0001-8434-4422
[4] ORCID ID: 0000-0002-6582-1219

https://doi.org/10.1016/j.gecco.2023.e02642
Received 21 March 2023; Received in revised form 4 September 2023; Accepted 15 September 2023
Available online 16 September 2023

1. Introduction

The harmful effects of increasing global temperature on biodiversity are well documented (Thomas et al., 2004; Butchart et al., 2010; Pecl et al., 2017). Since climatic conditions largely determine the geographical distribution of species, climate change has a large impact on biodiversity (Pearson and Dawson, 2003), not only by forcing species to shift their geographical ranges or driving local extinctions, but also by affecting the phenology or physiology of species, by changing community structures as well as ecosystem functions (Bellard et al., 2012). The disappearance of local, endemic taxa, as well as a reduced resistance and resilience of ecosystems are becoming more and more common due to climate change (Jump and Peñuelas, 2005). The general response of species to changing climatic conditions is to shift their range polewards or to higher altitudes (Parmesan and Yohe, 2003).

Whilst orchids are the most diverse and widespread family of flowering plants (Swarts and Dixon, 2009), they appear highly vulnerable to several factors, such as climate change, habitat destruction and disappearance of specific pollinators (Cribb et al., 2003; Kull and Hutchings, 2006). Moreover, orchids depend greatly on a diverse set of pollinators and mycorrhizal fungi (Waterman and Bidartondo, 2008), making them excellent biodiversity indicators (Swarts and Dixon, 2009). During the last 30 years, populations of several European terrestrial orchids have continued to decline due to climate change, habitat loss and/or fragmentation, thus, nowadays conservation efforts aiming to protect and preserve them are widespread (Sletvold et al., 2013). Orchids are influenced by climate change in several ways. First, precipitation deficiency could result in insufficient root development and limited nutrient storage (Rasmussen, 1995; Wells et al., 1998). Second, increased climate stochasticity could expose seedlings to heat shock and high temperatures could prevent orchids from finishing their vegetative life cycle successfully (Hutchings, 2010). Similarly, stochasticity in precipitation will likely affect terrestrial orchids, through imbalances in soil moisture (causing e.g., root rot or dehydration), vegetation and microclimate of habitats (Bates et al., 2008). Furthermore, extreme rainfall events can increase the probability of erosion, which might affect orchid populations growing on steep slopes. Due to these reasons, the attention of conservationists is increasingly turning towards the discovery of potential climatic refugia for species that might facilitate their survival under rising temperatures (Taberlet and Cheddadi, 2002; Hampe and Petit, 2005).

Despite the rarity and vulnerability of orchids, many species are known to colonize anthropogenic habitats in great numbers. Orchids produce microscopic seeds, that are effectively dispersed by the wind (Arditti and Ghani, 2000) facilitating the colonization of new habitat patches. This high dispersal potential could be a key reason explaining the high likelihood of orchid presence in disturbed anthropogenic habitats. Several anthropogenic areas were shown to provide habitat for orchids, including cemeteries (Löki et al., 2015, 2019a, 2019b; Molnár et al., 2017a, 2017b), poplar plantations (Süveges et al., 2019; Molnár V. et al., 2022), orchards (Delforge, 2006), abandoned mines (Esfeld et al., 2008; Shefferson et al., 2008), urban habitats (Rewicz et al., 2017), as well as roadsides (Fekete et al., 2017; Bódis et al., 2018; Fekete et al., 2019; Fekete et al., 2020). Roadside verges could serve as a new niche to be colonized by the wind-dispersed seeds of orchids. Furthermore, regular mowing of roadsides could facilitate the persistence of orchids of semi-natural grasslands (Fekete et al., 2017), since mowing in natural grasslands was also proved to be beneficial for orchid survival (Janečková et al., 2006; Sletvold et al., 2010). Colonization of roadsides by orchids has long been known in the Mediterranean region (Federici and Serpieri, 1868; Turrill, 1932; Brandes, 1988a, 1998b), while more recent evidence shows that the phenomenon is also present in Central- (Bódis et al., 2018; Fekete et al., 2020) and Northern-Europe (Gardiner and Vaughan, 2009). Roadside verges are generally only narrow grassland fragments, but they provide remarkably diverse environmental and microclimatic conditions. Consequently, roadsides can serve as habitats for a diverse set of orchid species with various habitat needs, including grassland- and forest-specialists, as well as species with wide ecological tolerance (Fekete et al., 2020).

Roadsides are generally categorized as small natural features (SNFs). Similarly, to other SNFs, such as midfield islets, burial mounds (Deák et al., 2016) or karst dolines (Bátori et al., 2019), roadsides are often characterized by a complex topography and a microclimate that differs from the surrounding areas, especially due to the special biotic and abiotic conditions at these sites (Deák et al., 2016; Hunter et al., 2017; Bátori et al., 2019). Special conditions mean that due to the slope steepness, the different exposition and growing light intensity, their vegetation often differs from the surroundings. Despite their limited spatial extent, SNFs have a great ecological importance, especially by providing refuge for various plant and animal species (Hunter et al., 2017). It was also reported that the special microclimate of SNFs has an important role in locally mitigating the negative effects of climate change (Keppel et al., 2012; Bátori et al., 2019). SNFs are often characterized by a great environmental heterogeneity, being one of the most important factors shaping biodiversity (Tamme et al., 2010). For instance, roadside slopes facing different compass directions often manifest highly different microclimates. Previous studies have shown remarkable difference in temperature (12 °C and 8 °C), between neighboring north- and south-facing slopes, suggesting a potential microrefugial role of roadsides (Rorison et al., 1986; Ackerly et al., 2010). McKee et al. (1965) showed a 40°F (4.4 °C) difference of the soil surface temperature between south- and north-facing highway slopes. Temperature is one of the most important climate element that depends on solar radiation, which is modified by the exposition of slopes. It means that insolation is the most intensive on slopes with southern exposition, while the least intensive on northern slopes (Bárány-Kevei, 1999).

However, the term "refugium" was originally referred to locations where a species survived the last glacial period, now this term is generally used in a wider sense: meaning areas (even small habitat patches) that are able to buffer the unfavorable effects of global climate change (Ashcroft, 2010). Climate refugia are considered as a "slow lane", which means areas that remain relatively buffered from the effects of climate change playing a vital role in retaining biodiversity and ecosystem function in a rapidly changing regional environment (Morelli et al., 2020). These refugia can safeguard species for longer periods, or, they can be transient, however, equally important, as they can sustain populations at the margins of species' distributions in a changing landscape (McLaughlin et al., 2017). Here we conduct a field survey of orchids on roadsides across 18 European countries over six years. The central aim of our study was to explore how local climatic or microclimatic conditions influence the presence of orchids on roadsides, and to test whether roadside slopes could function as microrefugia for orchids. We investigate whether orchids are countering the effect of unfavorable macroclimatic conditions by colonizing roadside slopes with more favorable microclimates. Therefore, we tested the following hypotheses: (1) The probability of orchid occurrence is higher in roadsides with northern exposure (in the northern hemisphere). (2) In regions of higher annual mean temperature, the probability of orchid occurrence will be lower on slopes of southern exposure, but higher on slopes of northern exposure. (3) In regions of higher precipitation seasonality, the probability of orchid occurrence will be lower on slopes of southern exposure, but higher on slopes of northern exposure. (4) In regions of higher annual precipitation, the probability of orchid occurrence will be higher, regardless of exposure.

2. Materials and methods

2.1. Road surveys

Road surveys were carried out between 2013 and 2018 in the following European countries: Albania, Austria, Bosnia and Herzegovina, Croatia, Cyprus, France, Greece (Crete and Lesbos), Hungary, Ireland, Italy, Kosovo, Montenegro, Romania, Serbia, Slovakia, Slovenia, Spain, United Kingdom. We used two types of sampling protocols. First, we conducted systematic sampling by driving along asphalt roads and we stopped at every 5 km (except in Lesbos, where we stopped at every 2 km due to the small area of the island). Second, we conducted non-systematic sampling, when we stopped at sites where orchids were spotted on the roadside while driving. Road segments were selected to be representative to the whole country regarding different elevations (except for three countries, Italy, Bosnia Herzegovina and Croatia, where we already knew the exact localities of *Himantoglossum* species on roadsides). We selected road segments where it was allowed to stop (we skipped motorways). Details of the sampling localities and sampling periods are given in Table 1. At every sampling point we recorded geographic coordinates (WGS84 format) and altitude (m) using a handheld Garmin E-Trex Legend GPS device. At each location, we registered the dominant exposure of the slope (in degrees) using a compass. Using these data, we later categorized exposure to the four (N, E, S, W) and eight (N, NE, E, SE, S, SW, W, NW) main compass points. At each sampling location, we surveyed roadsides for orchids on a 50 m long road section on both sides of the road (but in most cases only one side was a slope and the other was flat). The width of the surveyed roadside usually spanned 0.1–10 m, delimited by the roadway on one side and ditches, walls, or taller vegetation on the other. We recorded the presence/absence of orchids and where orchids were present, the number of specimens belonging to each detected species. Orchid species identification was done following Delforge (2006), and the nomenclature used in this study follows the same source. In some cases, identification of orchids to the species level was not possible due to their vegetative phenological state. In those cases, we counted the number of individuals, and were only considered in the overall count of orchid individuals.

2.2. Climatic data

Data on climate was extracted for each sampling point in our dataset from the WorldClim v.2 database (Fick and Hijmans, 2017), using a 2.5 min resolution. The bioclimatic variables are calculated from average monthly temperature and rainfall values between 1970 and 2000. Only three variables were chosen that were considered relevant, namely annual mean temperature (°C) (BIO1), annual precipitation (mm) (BIO12) and precipitation seasonality (coefficient of variation: the standard deviation of the monthly precipitation

Table 1
Summary of roadside surveys.

Country	Year of surveys	Number of non-systematic sampling points	Number of systematic sampling points	All sampling points
Hungary	2013–2015, 2017–2018	24	159	183
Croatia	2014, 2016	15	0	15
Albania	2015	7	0	7
Italy	2015, 2016	10	0	10
Bosnia and Herzegovina	2013–2015, 2017	13	0	13
Kosovo	2015	3	0	3
Montenegro	2015	18	0	18
Serbia	2015–2016	30	0	30
Ireland	2016	23	0	23
United Kingdom	2016	27	0	27
Cyprus	2016–2017	62	118	180
Spain	2016	30	0	30
France	2016	49	0	49
Austria	2017	0	51	51
Slovenia	2017	1	71	72
Slovakia	2017	0	88	88
Romania	2017	4	88	92
Greece (Crete, Lesbos)	2017–2018	72	323	395
Summary		388	898	1286

estimates expressed as a percentage of the mean of those estimates) (BIO15). Bioclimatic data was extracted using the raster (Hijmans and van Etten, 2012) and sp (Pebesma et al., 2012) packages in R v. 4.1.3 statistical software (R Core Team, 2022).

2.3. Data analyses

Data analyses were carried out in the R v. 4.1.3 statistical software (R Core Team, 2022). We built four generalized linear mixed models (GLMM) with binomial distribution using the package *merTools (*Knowles et al., 2016*)* and package *car* (Fox et al., 2012). In the models, presence/absence was the dependent variable, thus only the systematic data was used. First, to explore if orchids had an overall preference for certain slope exposures, we built a single-predictor GLMM. In this model we used exposure of slopes as a predictor (model 1). In case of model 1, differences in predictor levels were explored using Post-hoc Tukey tests performed using the *emmeans* R package (Lenth et al., 2020). Secondly, to test whether the probability of orchid occurrence is lower on slopes with southern exposure in regions where annual mean temperature was higher, we updated the base model. Here we used the interaction between the exposure of the slope and local annual mean temperature as a predictor (model 2). Third, to test whether in regions of higher precipitation seasonality the probability of orchid occurrence was lower on slopes of southern exposure, we built a model, where we used the interaction between the exposure of the slope and local precipitation seasonality as explanatory variable (model 3). Lastly, to determine whether annual precipitation affects the distribution of orchids across slopes with various exposure, we built a fourth model. Here we used the interaction between the exposure of the slope and local annual precipitation as explanatory variable (model 4). Thus, the effects of different cardinal directions were analyzed by including their interaction with the bioclimatic variables as predictors in the models. In case of the models where interactions were the predictors, we used *lstrends* functions from *lsmeans* R package (Lenth and Lenth, 2018) for pairwise comparisons.

For the analyses of the number of species, we built four (model 5,6,7,8) zero-inflated GLMMs with negative binomial error distribution, using the *glmmTMB* function (*glmmTMB* R package, Brooks et al., 2017). We used the number of species as a dependent variable and the same predictors and post-hoc tests as in the case of presence/absence models.

Finally, we built four (model 9,10,11,12) zero-inflated GLMMs with negative binomial error distribution, using also the *glmmTMB* function. We used the number of individuals as a dependent variable and the same predictors and post-hoc tests as in the case of the

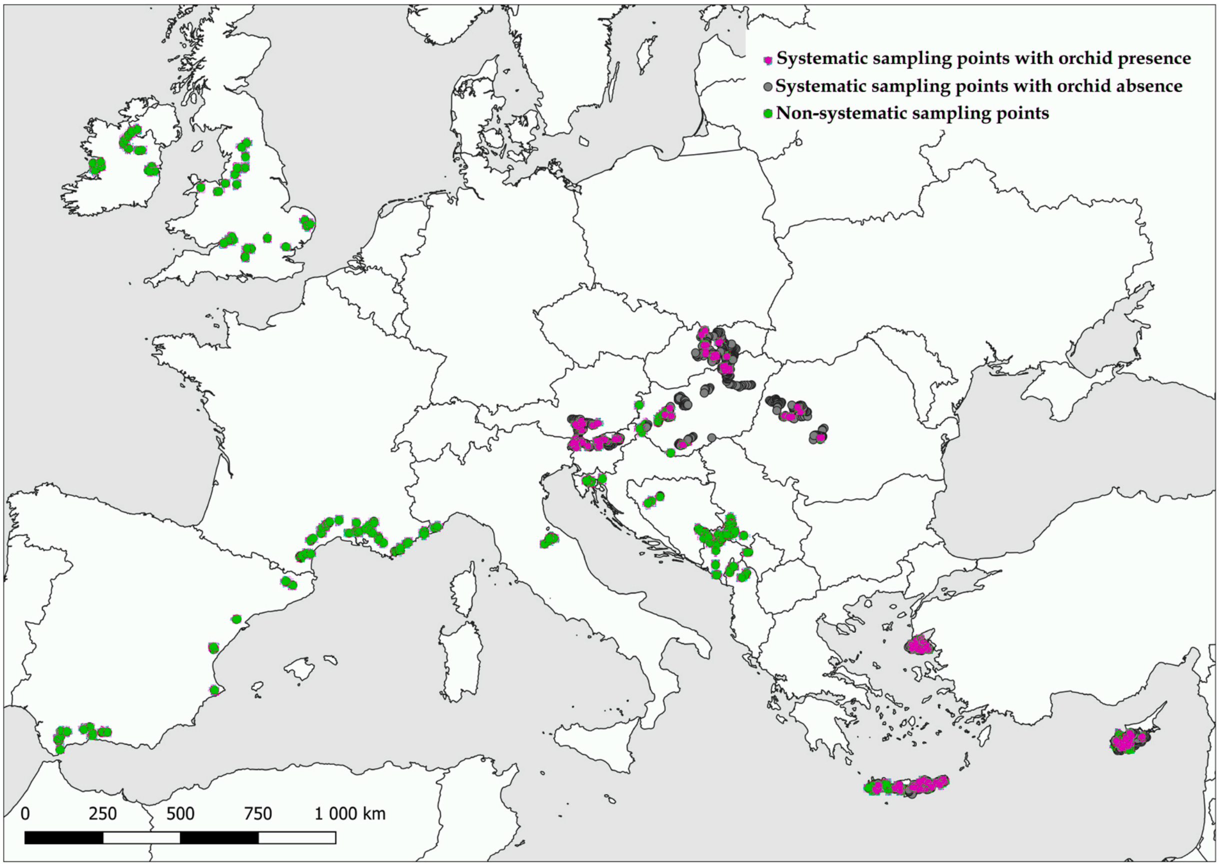

Fig. 1. Road surveys covering 18 European countries showing systematic sampling points (which were 5 km distance from each other including points with orchid presence and absence) and non-systematic sampling points (points where orchids were spotted from the car, in this way containing only sampling points with orchid presence).

above mentioned models. In all of the models, we used country as a random factor. In case of the zero-inflated models, we included the results of both the zero-inflated and conditional models in Table S3. Table S1 contain all underlying data analysed here.

3. Results

3.1. Overview of road surveys

During fieldwork we surveyed a total of 1286 sampling points (470 non-systematic and 816 systematic) in 18 European countries (Fig. 1). We found orchids at 238 (29 %) of the systematic sampling points. Overall, we documented 8531 individual orchids, belonging to 133 orchid taxa (Table S2). *Ophrys* was represented by the most diverse species set on roadsides, represented by 56 species, most of which were found in the Mediterranean region. *Dactylorhiza fuchsii* was the most abundant species in roadsides in six countries, with a total number of 1014 individuals recorded. *Himantoglossum robertianum* was the most frequently registered species across sampling points (100 non-systematic and systematic, combined), but it was found in only three countries. *Neottia ovata* was the most widespread species found in 12 countries. The species diversity of orchids detected in some countries was remarkably high, in Cyprus we found 20 orchid species at roadsides that represented the 38% of the island's orchid flora.

Orchid taxa of high conservation importance detected on roadsides include endangered species, such as *Epipactis veratrifolia*, *Gymnadenia austriaca* and *G. lithopolitanica*, vulnerable species like *Orchis boryi* and *O. punctulata* or the near threatened *Epipactis microphylla, Limodorum abortivum* var. *trabutianum*, *Orchis morio* and *Ophrys kotschyi* (IUCN, 2021). Furthermore, we found a number of locally rare orchid taxa at roadsides, including *Gymnadenia* × *suaveolens* in Austria or *Orchis mascula* in Slovakia, a species that is near threatened according to the Red List of vascular plants of the Carpathian part of Slovakia (Turis et al., 2014). Additionally, we documented *Platanthera chlorantha* in roadsides of Hungary, a species listed as near threatened according to the Red list of the vascular flora of Hungary (Király, 2007).

Orchids were most numerous on north-facing slopes represented by 1979 individuals, followed by 1255 individuals on west-facing slopes, 942 on east-facing and 596 individuals on south-facing slopes. (Fig. 2.). The rest of the individuals (3759) were found at flat sites, not exposed to any particular compass direction.

3.2. Microclimatic analyses

3.2.1. Probability or presence

Table S3 contains the results of all models. We found a significant difference between the probability of presence of orchids in the four cardinal directions. Post-hoc tests indicated that probability of presence was significantly higher in slopes with northern exposure than on south-facing ones (z-ratio = 4.781, p < .0001). (Fig. 3). No significant differences were detected between other cardinal directions during pairwise comparisons.

Binomial GLM (model 2) showed a marginally significant interaction between annual mean temperature and slope exposure,

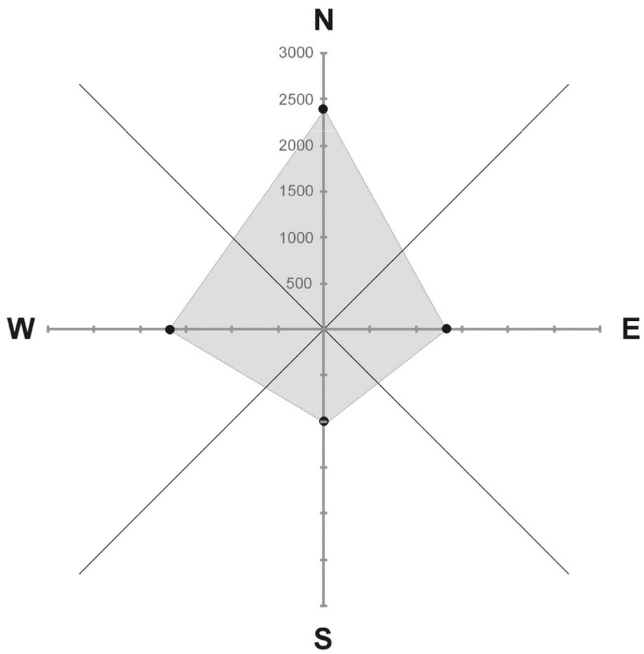

Fig. 2. Number of orchid individuals documented in roadside slopes at four cardinal directions.

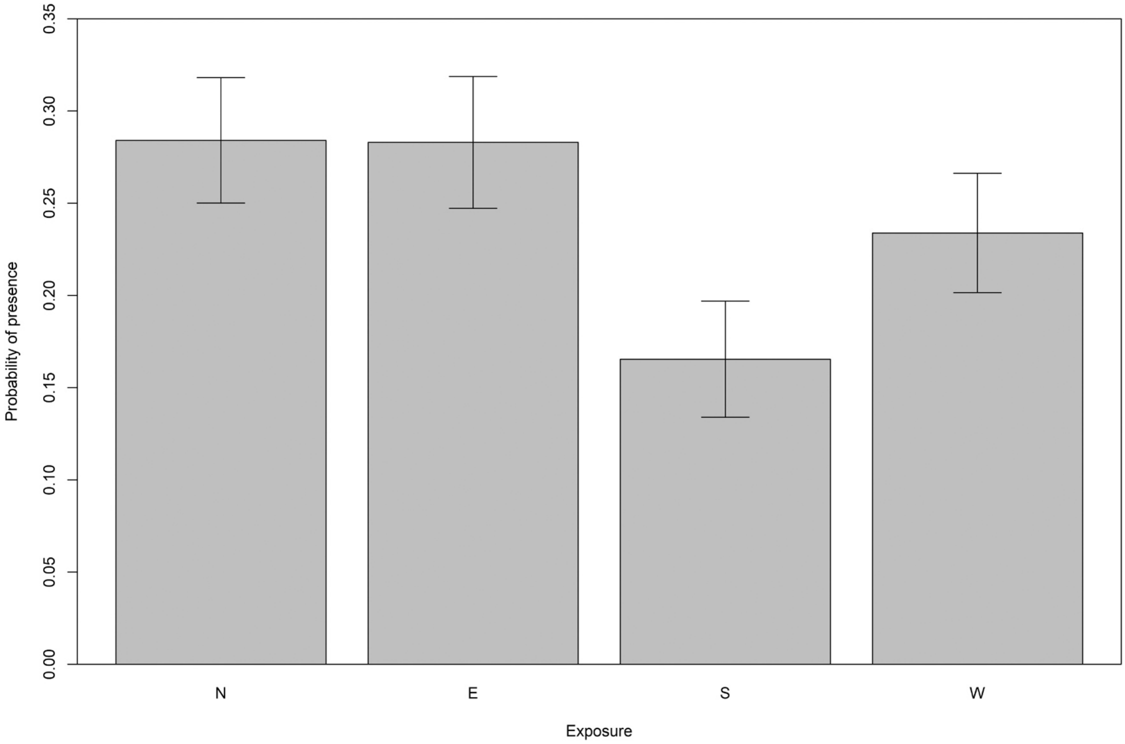

Fig. 3. Probability of orchid occurrence in four cardinal directions.

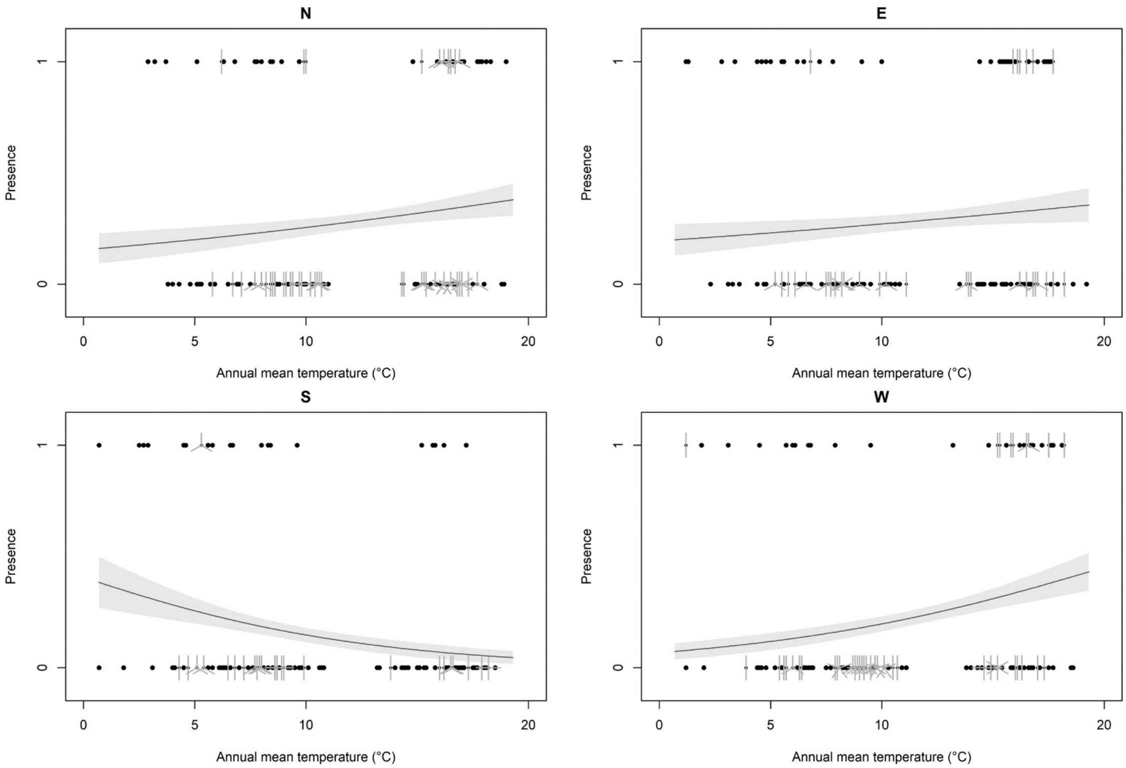

Fig. 4. Probability of orchid occurrence in function of annual mean temperature at four cardinal directions.

indicating that orchids reacted differently to regional temperatures on south-facing slopes than on slopes facing any other compass direction (Fig. 4). The probability of orchid occurrence increased with higher regional temperatures in northern, western and eastern exposures, but decreased with increasing regional temperatures on south-facing roadside slopes. Pairwise comparison indicated that southern slopes differed significantly from western slopes ($p = 0.011$). No other significant difference was detected during pairwise comparison.

Binomial GLM (model 3) showed a marginal significant interaction between precipitation seasonality and slope exposure. The probability of orchid occurrence sharply decreased with higher extent of precipitation seasonality in southern exposures (Fig. 5). According to pairwise comparisons, a significant difference can be detected between southern and western slopes ($p = 0.009$).

We found no significant interaction between exposure and annual precipitation (model 4), but annual precipitation itself marginally significantly positively affected the presence of orchids. All models are shown in Table S4.

3.2.2. *Number of species*

Results of all the models are shown in Table S3. Number of species was significantly higher on northern than southern or eastern slopes (model 5 and post-hoc test) (Fig. 6). Interaction of exposure and temperature (model 6) and the interaction of exposure and precipitation seasonality (model 7) showed a marginally significant difference of western slopes from northern slopes but post-hoc test showed no significant differences. In case of annual precipitation (model 8) we found no significant or marginally significant interaction with exposure.

3.2.3. *Number of individuals*

According to model 9 and the post-hoc test, the number of individuals was significantly higher in northern slopes than in any other directions (Fig. 7, Table S3.).

Interaction of exposure and temperature (model 10) and the interaction of exposure and precipitation seasonality (model 11) was marginally significantly different. Number of individuals reacted differently to regional temperature and precipitation seasonality on western and southern slopes than the number of individuals on northern slopes but the post-hoc test showed no significant differences. In case of annual precipitation (model 12), we found no significant or marginally significant interaction with exposure.

4. Discussion

Our article presents the largest scale survey of orchids along roadsides to date, regarding the surveyed number of countries and sampling points. Using this wide-scale European survey we make three important conclusions. First, roadsides harbor an important and diverse set of terrestrial orchids, many with top conservation importance (Table S3), since more than 8080 individuals and 130

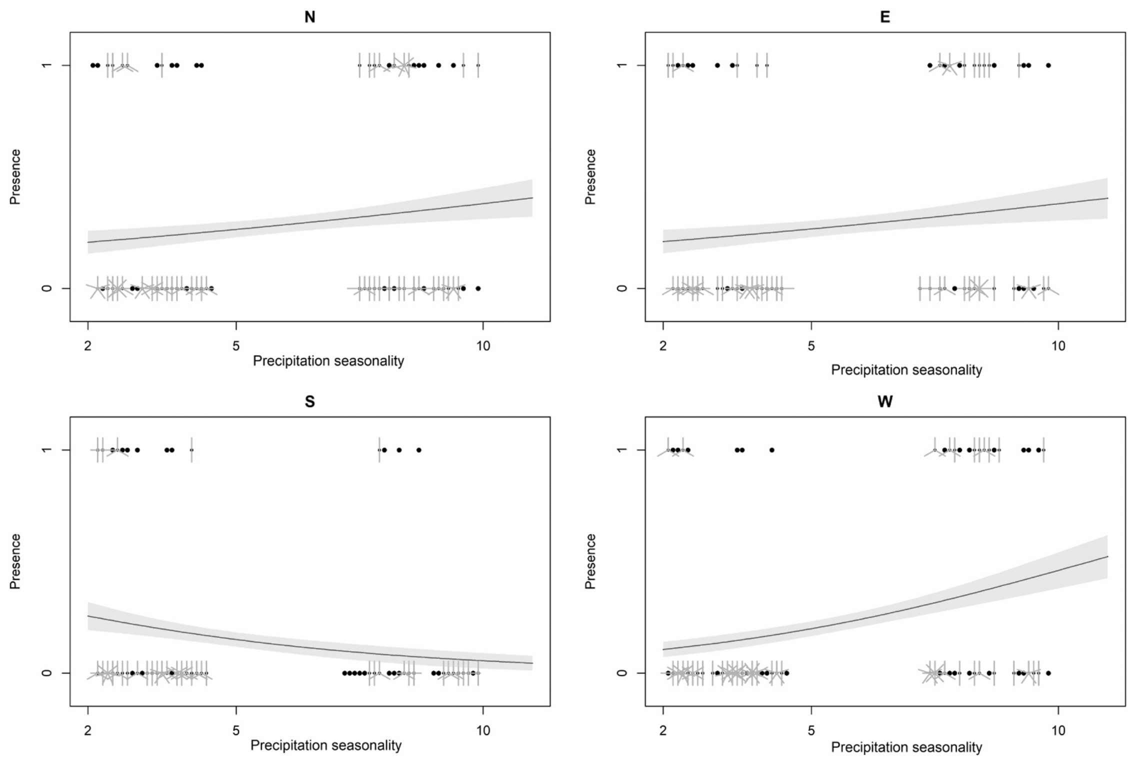

Fig. 5. Probability of orchid occurrence as a function of precipitation seasonality in four cardinal directions.

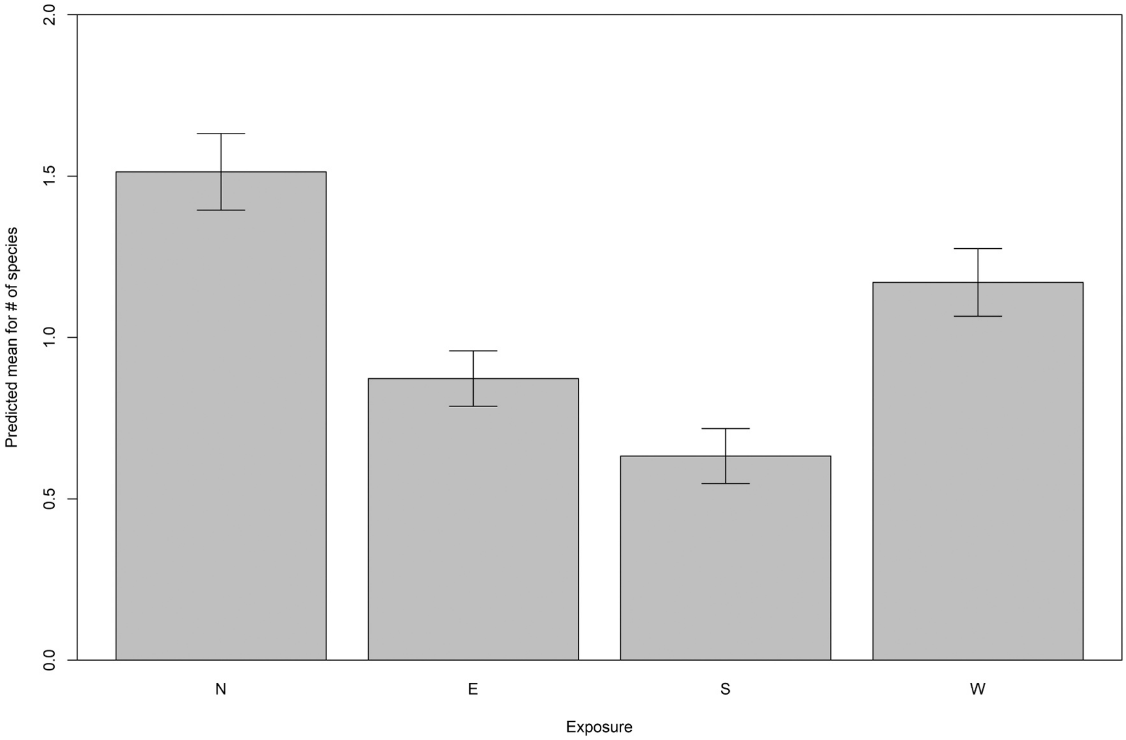

Fig. 6. Predicted mean of number of species in four cardinal directions.

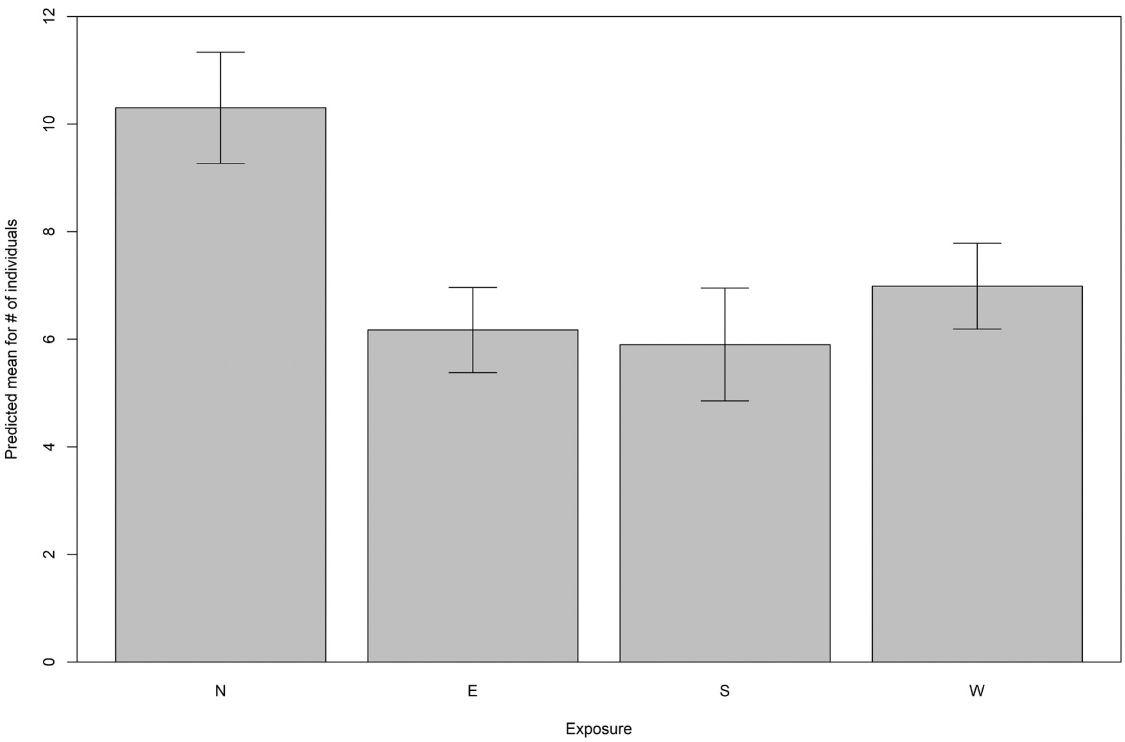

Fig. 7. Predicted mean of number of individuals in four cardinal directions.

different orchid taxa were found on roadsides during our surveys. Second, we show that abiotic conditions of roadside slopes determine their suitability for orchids, since the results of this study pointed out that north-facing roadside slopes have the highest probability to harbor orchids and maintained the highest number of species and individuals. Third, we showed an effect of the interaction between slope exposure and annual mean temperature as well as of the interaction between slope exposure and precipitation seasonality on orchid presence, the number of species and also the number of individuals. These results suggest that south-facing slopes amplify the negative effect of high regional temperature and high precipitation seasonality creating unfavorable habitats for orchids.

South-facing roadside slopes had a lower probability to support orchids. Many orchids are specialists, and in very dry (e.g., south-facing) conditions they cannot compete with generalists or weeds, and their disappearance leads to functional homogenization in ecosystems (Clavel et al., 2011). Similar conclusions were reached by Deák et al. (2021) showing that south- and east-facing kurgan slopes were more dominantly covered by weeds and generalists, while specialist species were more common in north- and west-facing slopes. According to the latter work the clear difference in species composition between north- and south-facing slopes of kurgans is potentially the result of different microclimates on these. North- and west-facing slopes were characterized by mild conditions, ideal for specialist plant species, while south- and east-facing slopes were characterized by harsher conditions, giving space for weeds and more disturbance tolerant species. Bátori et al. (2019) also reported a very clear difference between the microclimate of north- and south-facing slopes of karst dolines, showing an 8 °C difference between the two opposite exposures, suggesting the microrefugial role of the dolines against climate change. Although we did not conduct microclimatic measurements, the previous studies suggest that opposite slopes of roadsides might be characterized by remarkable microclimatic differences.

It is well-known that climatic factors strongly influence orchid performance (Djordjević and Tsiftsis, 2022). According to our results, orchids colonize south-facing roadside slopes with a lower probability at sites where the annual mean temperature was higher. Although the effect of temperature on plants at a finer scale can vary from species to species (Blinova et al., 2003), our findings suggest that orchids find shelter in cooler (north- and west-facing) roadside slopes under unfavorable macroclimatic conditions, such as high temperatures.

Precipitation seasonality affects vegetation in several ways, leading to water stress, reduced biomass and altered phenology (Zeppel et al., 2013). Previous studies show that precipitation seasonality was one of the significant predictors, showing negative effect on the occurrence of two orchid species, *Neottia cordata* and *Ophrys argolica*, highlighting the importance of summer rainfall (Tsiftsis et al., 2019; Tsiftsis and Djordjević, 2020). Nevertheless, we found that the probability of orchid occurrence was lower under higher precipitation seasonality in south-facing roadside slopes, suggesting that under dry microclimatic conditions negative effects of climate change are exacerbated.

Our results also indicate that annual precipitation generally and positively influenced orchid occurrence. Precipitation affects population dynamics, flowering period, the height of the stem and inflorescence or the number of flowers of orchids (Wells and Cox, 1991). The number of flowering specimens of *Himantoglossum adriaticum* was positively correlated with the amount of rainfall in the previous growing season (Bódis et al., 2019), while the flowering of *Herminium monorchis, Dactylorhiza sambucina*, *Neottia ovata and Gymnadenia conopsea* negatively correlated with summer drought (Wells, 1981; Inghe and Tamm, 1988; Øien and Moen, 2002). Interactions of precipitation and exposure did not have an effect on orchid presence, suggesting that severe negative effects of drought might affect orchids regardless of exposure.

Although this study focused on orchids, we should emphasize that there might be other species, in other regions that thrive on south-facing roadside slopes. For example, in the Czech Republic steppe species and steppe-like habitats are maintained on south-facing roadside slopes (Heneberg et al., 2017).

5. Conclusions

We conclude that shadier and more humid north-, west- or east-facing roadside slopes could potentially mitigate the negative effects of climate change and might facilitate the survival of orchids at unfavorable macroclimatic conditions. Roadsides are usually managed in a way that is suitable for orchid conservation. Their role in the survival of plant species under global climate change might be enhanced, since they are considered to act as ecological corridors facilitating species dispersal through fragmented and transformed landscapes and to find shelter while adapting to a changing climate. Further research should focus on how pollinators are adapting to the changing climate, utilizing microclimatic measurements, in order to promote orchid reproductive success and long-term survival.

6. Implications for management

The most important before road construction projects is the floristic survey of roadsides and adjacent areas to consider local conservation efforts. When roads are planned to be broadened, in areas where orchid conservation should be enhanced, according to our results and previous ones, north- and west-facing sides should not be destroyed due to their role in the maintenance of orchid diversity. Furthermore, wider roadside verges should be designed to facilitate the persistence of pollinators, since the proximity of roads enhances their collision with cars (Hopwood et al., 2010; Keilsohn et al., 2018). Topographically diverse landscapes or habitat islands can mitigate local extinctions, therefore, it is likely that the importance of western and northern roadside slopes will grow in the future (Keppel et al., 2012). Even though some roadsides harboring rare and threatened plants are already managed in a way to preserve these, we suggest to designate roadsides with high biodiversity as "Roadside Nature Reserves", which is a practice already used in the United Kingdom (Atherden et al., 2018; Kent Wildilife Trust, 2022). These Roadside Nature Reserves should be managed appropriately with the help of public road managers and national parks to maintain species richness and support landscape-scale biodiversity.

Funding

This research was supported by NKFIH-OTKA K132573 Grant. RF was supported by NKFIH-OTKA PD143425 and by the New National Excellence Program of the Hungarian Ministry for Innovation and Technology (ÚNKP-20-3-II-DE-17). OV was financed by the National Scientific Research Fund (OTKA K143421) and by a grant of the Romanian Ministry of Research, Innovation and Digitization (CNCS - UEFISCDI, project number PN-III-P1-1.1-TE-2021-0502).

CRediT authorship contribution statement

Réka Fekete: Data curation; Formal analysis; Investigation; Methodology; Resources; Visualization; Writing - original draft; **Orsolya Vincze:** Formal analysis, Visualization, Writing – Review & Editing; **Jenő Nagy:** Formal analysis, Visualization, Writing – Review & Editing; **Viktor Löki:** Investigation, Visualization, Writing – Review & Editing; **Kristóf Süveges:** Investigation, Writing – Review & Editing; **Judit Bódis:** Investigation, Writing – Review & Editing; **Tamás Malkócs**: Investigation, Formal analysis, Writing – Review & Editing; **Ádám Lovas-Kiss**: Investigation, **Attila Molnár V.:** Conceptualization, Investigation, Resources, Writing – Review & Editing, Supervision, Funding acquisition, Visualization.

Declaration of Competing Interest

The authors have no conflicts of interest or competing interest.

Data Availability

Data will be made available on request.

Acknowledgements

The authors are grateful to Éva Biró, Bence Fülöp, Ildikó Juhász, Tímea Nagy, Zsófia Simon, Attila Takács and Renáta Urgyán for their help during field work.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02642.

References

Ackerly, D.D., Loarie, S.R., Cornwell, W.K., Weiss, S.B., Hamilton, H., Branciforte, R., Kraft, N.J.B., 2010. The geography of climate change: implications for conservation biogeography. Divers. Distrib. 16, 476–487. https://doi.org/10.1111/j.1472-4642.2010.00654.x.

Arditti, J., Ghani, A.K.A., 2000. Tansley Review No. 110. Numerical and Physical Properties of Orchid Seeds and Their Biological Implications. New Phytol 145 (3), 367–421. https://doi.org/10.1046/j.1469-8137.2000.00587.x.

Ashcroft, M.B., 2010. Identifying refugia from climate change. J. Biogeogr. 37, 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x.

Atherden, M., Rotherham, I.D., Handley, C., 2018. Roadside assistance: Management and conservation of North Yorkshire's wayside flowers. Back from the Edge: The Fall & Rise of Yorkshire's Wildlife, 73–82.

Bárány-Kevei, I., 1999. Microclimate of karstic dolines. Acta Climatol. 32 (33), 19–27.

Bates, B., Kundzewicz, Z., Wu, S., 2008. Climate change and water. Intergovernmental Panel on Climate Change Secretariat. ⟨http://www.taccire.sua.ac.tz/handle/123456789/552⟩.

Bátori, Z., Vojtkó, A., Maák, I.E., Lőrinczi, G., Farkas, T., Kántor, N., Tanács, E., Kiss, P.J., Juhász, O., Módra, G., Tölgyesi, C., Erdős, L., Aguilon, D.J., Keppel, G., 2019. Karst dolines provide diverse microhabitats for different functional groups in multiple phyla. Sci. Rep. 9, 7176. https://doi.org/10.1038/s41598-019-43603-x.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., Courchamp, F., 2012. Impacts of climate change on the future of biodiversity. Ecol. Lett. 15, 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x.

Blinova, I.V., Willems, J.H., van Reenen, J., 2003. Intraspecific variation in orchid populations in two different climatic areas in Europe, Murmansk Region and the Netherlands. J. Eur. Orch.. 35, 79–99.

Bódis, J., Biró, É., Nagy, T., Takács, A., Molnár, V., A., Lukács, B.A., 2018. Habitat preferences of the rare lizard-orchid *Himantoglossum adriaticum* H. Baumann. Tuexenia 38, 329–345. https://doi.org/10.14471/2018.38.020.

Bódis, J., Biró, É., Nagy, T., Takács, A., Sramkó, G., Bateman, R.M., Gilián, L., Illyés, Z., Tökölyi, J., Lukács, B.A., Csábi, M., Molnár, A.V., 2019. Biological Flora of Central Europe: *Himantoglossum adriaticum* H. Baumann. Perspect. Plant Ecol. Evol. Syst., 125461 https://doi.org/10.1016/j.ppees.2019.125461.

Brandes, D., 1998a. Vegetation der Straßenränder Korfus. – Vegetationsökologie von Habitatinseln und linearen Strukturen. Braunschw. Geobot. Arb. 5, 247–262.

Brandes, D., 1998b. Flora und Vegetation der Straßenränder von Mallorca. – Vegetationsökologie von Habitatinseln und linearen Strukturen. Braunschw. Geobot. Arb. 5, 275–293.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Bolker, B.M., 2017. Modeling zero-inflated count data with glmmTMB. BioRxiv, 132753.

Butchart, S.H.M., Walpole, M., Collen, B., Van Strien, A., Scharlemann, J.P., Almond, R.E., Baillie, J.E., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., 2010. Global biodiversity: indicators of recent declines. Science 5982, 1164–1168. https://doi.org/10.1126/science.1187512.

Clavel, J., Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 94, 222–228. https://doi.org/10.1890/080216.

Cribb, P.J., Kell, S.P., Dixon, K.W., Barrett, R.L., 2003. Orchid conservation: a global perspective. In: Dixon, K.W., Kell, S.P., Barrett, R.L., Cribb, P.J. (Eds.), Orchid Conservation. Natural History Publications, Kota Kinabalu, Sabah, pp. 1–24.

Deák, B., Tóthmérész, B., Valkó, O., Sudnik-Wójcikowska, B., Bragina, T.M., Moysiyenko, I.I., Apostolova, I., Dembicz, I., Bykov, N.I., Török, P., 2016. Cultural monuments and nature conservation: the role of kurgans in maintaining steppe vegetation. Biodiv. Conserv. 25, 2473–2490. https://doi.org/10.1007/s10531-016-1081-2.

Deák, B., Kovács, B., Rádai, Z., Apostolova, I., Kelemen, A., Kiss, R., Lukács, K., Palpurina, S., Sopotlieva, D., Báthori, F., Valkó, O., 2021. Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. Sci. Total Environ. 763, 144199 https://doi.org/10.1016/j.scitotenv.2020.144199.

Delforge, P., 2006. Orchids of Europe, North Africa and the Middle East. A and C Black Publishers Ltd, London.

Djordjević, V., Tsiftsis, S., 2022. The role of ecological factors in distribution and abundance of terrestrial orchids. In: Orchids phytochemistry, biology and horticulture: fundamentals and applications. Springer International Publishing, Cham, pp. 3–72.

Esfeld, K., Hensen, I., Wesche, K., Jakob, S.S., Tischew, S., Blattner, F.R., 2008. Molecular data indicate multiple independent colonizations of former lignite mining areas in Eastern Germany by *Epipactis palustris* (Orchidaceae). Biodiv. Conserv. 17, 2441–2453. https://doi.org/10.1007/s10531-008-9391-7.

Federici, A., Serpieri, A., 1868. Saggio di una Flora dell'agro urbinate ed epoca della fioritura di molte piante. Bull. Met. Urbino 2, 32–38.

Fekete, R., Löki, V., Urgyán, R., Süveges, K., Lovas-Kiss, Á., Vincze, O., Molnár, V., A., 2019. Roadsides and cemeteries: comparative analysis of anthropogenic orchid habitats in the Eastern Mediterranean. Ecol. Evol. 9, 6655–6664. https://doi.org/10.1002/ece3.5245.

Fekete, R., Nagy, T., Bódis, J., Biró, É., Löki, V., Süveges, K., Takács, A., Tökölyi, J., Molnár, V., A., 2017. Roadsides as habitats for endangered lizard-orchids (*Himantoglossum* spp.): Ecological traps or refuges? Sci. Total Environ. 607, 1001–1008. https://doi.org/10.1016/j.scitotenv.2017.07.037.

Fekete, R., Bódis, J., Fülöp, B., Süveges, K., Urgyán, R., Malkócs, T., Vincze, O., Luís, S., Molnár, V., A., 2020. Roadsides provide refuge for orchids: characteristic of the surrounding landscape. Ecol. Evol. 10, 13236–13247. https://doi.org/10.1002/ece3.6920.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315.

Fox, J., Weisberg, S., Adler, D., Bates, D., Baud-Bovy, G., Ellison, S., Heiberger, R., 2012. Package 'car'. Vienna: R Foundation for Statistical Computing.

Gardiner, T., Vaughan, A., 2009. Scrub clearance and soil disturbance increases bee orchid *Ophrys apifera* frequency in calcareous grassland at Norton Heath roadside verge. Essex, Engl. Conserv. Evid. 6, 39–41.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461–467. https://doi.org/10.1111/j.1461-0248.2005.00739.x.

Heneberg, P., Bogusch, P., Řezáč, M., 2017. Roadside verges can support spontaneous establishment of steppe-like habitats hosting diverse assemblages of bees and wasps (Hymenoptera: Aculeata) in an intensively cultivated central European landscape. Biodiv. Conserv. 26, 843–864.

Hijmans, R.J., van Etten J., 2012. raster: Geographic analysis and modeling with raster data. R package version 2.0–12.

Hopwood, J., Winkler, L., Deal, B., Chivvis, M., 2010. Use of roadside prairie plantings by native bees. Living Roadway Trust Fund [online] URL: http://www.iowalivingroadway. com/ResearchProjects/90–00-LRTF-011.pdf (accessed 19 April 2020).

Hunter, M.L., Acuña, V., Bauer, D.M., Bell, K.P., Calhoun, A.J.K., Felipe-Lucia, M.R., Fitzsimons, J.A., González, E., Kinnison, M., Lindenmayer, D., Lundquist, C.J., Medellin, R.A., Nelson, E.J., Poschlod, P., 2017. Conserving small natural features with large ecological roles: a synthetic overview. Biol. Conserv 211, 88–95. https://doi.org/10.1016/j.biocon.2016.12.020.

Hutchings, M.J., 2010. The population biology of the early spider orchid *Ophrys sphegodes* Mill. III. Demography over three decades. J. Ecol. 98, 867–878. https://doi.org/10.1111/j.1365-2745.2010.01661.x.

Inghe, O., Tamm, C.O., 1988. Survival and flowering of perennial herbs. V. Patterns of flowering. Oikos 51, 203–219. https://doi.org/10.2307/3565644.

IUCN, 2021. The IUCN Red List of Threatened Species. Version 2021–3. https://www.iucnredlist.org. (accessed 03 March 2022).

Janečková, P., Wotavová, K., Schödelbauerová, I., Jersáková, J., Kindlmann, P., 2006. Relative effects of management and environmental conditions on performance and survival of populations of a terrestrial orchid, *Dactylorhiza majalis*. Biol. Conserv. 129, 40–49. https://doi.org/10.1016/j.biocon.2005.09.045.

Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8, 1010–1020. https://doi.org/10.1111/j.1461-0248.2005.00796.x.

Keilsohn, W., Narango, D.L., Tallamy, D.W., 2018. Roadside habitat impacts insect traffic mortality. J. Insect Conserv 22, 183–188. https://doi.org/10.1007/s10841-018-0051-2.

Kent Wildilife Trust 2022. https://www.kentwildlifetrust.org.uk/ (accessed: 22 April 2022).

Keppel, G., Van Niel, K.P., Wardell-Johnson, G.W., Yates, C.J., Byrne, M., Mucina, L., Antonius, G.T.S., Stephen, D.H., Franklin, S.E., 2012. Refugia: identifying and understanding safe havens for biodiversity under climate change. Glob. Ecol. Biogeogr. 21, 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x.

Király, G. 2007. Red list of the vascular flora of Hungary. Private Edition, Sopron.

Knowles, J.E., Frederick, C., Whitworth, A., Knowles, M.J.E., 2016. Package 'merTools'.

Kull, T., Hutchings, M.J., 2006. A comparative analysis of decline in the distribution ranges of orchid species in Estonia and the United Kingdom. Biol. Conserv. 129, 31–39. https://doi.org/10.1016/j.biocon.2005.09.046.

Lenth, R., Lenth, M.R., 2018. Package 'lsmeans'. Am. Stat. 34, 216–221.

Lenth, R., Singmann, H., Love, J., Buerkner, P., Herve, M., 2020. emmeans: estimated marginal means. R package version 1.4. 4. Am. Stat. 34, 216–221.

Löki, V., Deák, B., Lukács, B.A., Molnár, V., A., 2019b. Biodiversity potential of burial places – a review on the flora and fauna of cemeteries and churchyards. Glob. Ecol. Conserv. 18, 00614. https://doi.org/10.1016/j.gecco.2019.e00614.

Löki, V., Tökölyi, J., Süveges, K., Lovas-Kiss, Á., Hürkan, K., Sramkó, G., Molnár V, A., 2015. The orchid flora of Turkish graveyards: a comprehensive field survey. Willdenowia 45, 231–243. https://doi.org/10.3372/wi.45.45209.

Löki, V., Molnár, V., A., Süveges, K., Heimeier, H., Takács, A., Nagy, T., Fekete, R., Lovas-Kiss, Á., Kreutz, C.A.J., Sramkó, G., Tökölyi, J., 2019a. Predictors of conservation value of Turkish cemeteries: a case study using orchids. Landsc. Urban Plan. 186, 36–44. https://doi.org/10.1016/j.landurbplan.2019.02.016.

McKee, W.H., Powell, A.J., Cooper, R.B., Blaser, R.E., 1965. Microclimate conditions found on highway slope facings as related to adaptation of species. Highw. Res. Rec. 93, 38–43.

McLaughlin, B.C., Ackerly, D.D., Klos, P.Z., Natali, J., Dawson, T.E., Thompson, S.E., 2017. Hydrologic refugia, plants, and climate change. Glob. Change Biol. 23, 2941–2961.

Molnár, V., A., Takács, A., Mizsei, E., Löki, V., Barina, Z., Sramkó, G., Tökölyi, J., 2017a. Religious differences affect orchid diversity of Albanian graveyards. Pak. J. Bot. 49, 289–303.

Molnár, V., A., Nagy, T., Löki, V., Süveges, K., Takács, A., Bódis, J., Tökölyi, J., 2017b. Turkish graveyards as refuges for orchids against tuber harvest. Ecol. Evol. 7, 11257–11264. https://doi.org/10.1002/ece3.3562.

Molnár V, A., Süveges, K., Fekete, R., Archaux, F., Chevalier, R., Takács, A., 2022. Orchids of poplar plantations – a review. Kitaibelia. https://doi.org/10.17542/kit.27.012.

Morelli, T.L., Barrows, C.W., Ramirez, A.R., Cartwright, J.M., Ackerly, D.D., Eaves, T.D., Ebersole, J.L., Krawchuk, A.M., Letcher, H.B., Mahalovich, M.F., Meigs, G.W., Michalak, J.L., Millar, I.C., Quiñones, M.R., Stralberg, D., Thorne, J.H., 2020. Climate-change refugia: biodiversity in the slow lane. Front. Ecol. Environ. 18 (5), 228–234. https://doi.org/10.1002/fee.2189.

Øien, D.I., Moen, A., 2002. Flowering and survival of *Dactylorhiza lapponica* and *Gymnadenia conopsea* in the Solendet nature reserve, Central Norway. In: Kindlmann, P., Willems, J.H., Whigham, D.F. (Eds.), Trends and Fluctuations And Underlying Mechanisms In Terrestrial Orchid Populations. Backhyus Publishers, Leiden, pp. 3–22.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42. https://doi.org/10.1038/nature01286.

Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Glob. Ecol. Biogeogr. 12, 361–371. https://doi.org/10.1046/j.1466-822x.2003.00042.x.

Pebesma, E., Bivand, R., Pebesma, M.E., R Color Brewer, S., Collate, A.A.A., 2012. Package 'sp'. The Comprehensive R Archive Network.

Pecl, G., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.C., Clark, T.D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human wellbeing. Science 355, 9214. https://doi.org/10.1126/science.aai9214.
R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org/.
Rasmussen, H.N., 1995. Terrestrial Orchids: From Seed to Mycotrophic Plant. Cambridge University Press.
Rewicz, A., Bomanowska, A., Shevera, M.V., Kurowski, J.K., Krasoń, K., Zielińska, K.M., 2017. Cities and disturbed areas as man-made shelters for orchid communities. Not. Bot. Horti Agrobot. Cluj. -Napoca 45, 126–139. https://doi.org/10.15835/nbha45110519.
Rorison, I.H., Sutton, F., Hunt, R., 1986. Local climate, topography and plant growth in Lathkill Dale NNR. I. A twelve-year summary of solar radiation and temperature. Plant Cell Environ. 9, 49–56. https://doi.org/10.1111/1365-3040.ep11612961.
Shefferson, R.P., Kull, T., Tali, K., 2008. Mycorrhizal interactions of orchids colonizing Estonian mine tailings hills. Am. J. Bot. 95, 156–164. https://doi.org/10.3732/ajb.95.2.156.
Sletvold, N., Øien, D.I., Moen, A., 2010. Long-term influence of mowing on population dynamics in the rare orchid *Dactylorhiza lapponica*: the importance of recruitment and seed production. Biol. Conserv. 143 747–755. https://doi.org/10.1016/j.biocon.2009.12.017.
Sletvold, N., Dahlgren, J., Øien, D., Moen, A., Ehrlén, J., 2013. Climate warming alters effects of management on population viability of threatened species: results from a 30-year experimental study on a rare orchid. Glob. Change Biol. 19, 2729–2738. https://doi.org/10.1111/gcb.12167.
Süveges, K., Löki, V., Lovas-Kiss, Á., Ljubka, T., Fekete, R., Takács, A., Vincze, O., Lukács, B.A., Molnár, V., A., 2019. From European priority species to characteristic apophyte: *Epipactis tallosii* (Orchidaceae). Willdenowia 49, 401–409. https://doi.org/10.3372/wi.49.49310.
Swarts, N.D., Dixon, K.W., 2009. Terrestrial orchid conservation in the age of extinction. Ann. Bot. 104, 543–556. https://doi.org/10.1093/aob/mcp025.
Taberlet, P., Cheddadi, R., 2002. Quaternary refugia and persistence of biodiversity. Science 297, 2009–2010. https://doi.org/10.1126/science.297.5589.2009.
Tamme, R., Hiiesalu, I., Laanisto, L., Szava-Kovats, R., Pärtel, M., 2010. Environmental het- erogeneity, species diversity and co-existence at different spatial scales. J. V. Sci. 21, 796–801. https://doi.org/10.1111/j.1654-1103.2010.01185.x.
Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F., De Siqueira, M.F., Gringer, A., Hannah, L., Huges, L., Huntley, B., Van Jarrsveld, A.S., Midgley, G.F., Miles, L., Ortega-Hueta, M.A., Petersen, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148. https://doi.org/10.1038/nature02121.
Tsiftsis, S., Djordjević, V., 2020. Modelling sexually deceptive orchid species distributions under future climates: the importance of plant–pollinator interactions. Sci. Rep. 10, 1–12. https://doi.org/10.1038/s41598-020-67491-8.
Tsiftsis, S., Djordjević, V., Tsiripidis, I., 2019. *Neottia cordata* (Orchidaceae) at its southernmost distribution border in Europe: Threat status and effectiveness of Natura 2000 Network for its conservation. J. Nat. Conserv. 48, 27–35. https://doi.org/10.1016/j.jnc.2019.01.006.
Turis, P., Kliment, J., Feráková, V., Dítě, D., Eliáš, P., Hrivnák, R., Košťál, J., Šuvada, R., Mráz, P., Bernátová, D., 2014. Red List of vascular plants of the Carpathian part of Slovakia. Thaiszia – J. Bot. 24, 35–87.
Turrill, W.B., 1932. On the Flora of the Nearer East: XI. A contribution to the flora of Albania. Bull. Misc. Inf. 1932 (4), 193–198.
Waterman, R.J., Bidartondo, M.I., 2008. Deception above, deception below: linking pollination and mycorrhizal biology of orchids. J. Exp. Bot. 59, 1085–1096. https://doi.org/10.1093/jxb/erm366.
Wells, T.C.E., 1981. Population ecology of terrestrial orchids. In: Synge, H. (Ed.), The biological aspects of rare plant conservation. Wiley, Chichester.
Wells, T.C.E., Rothery, P., Cox, R., Bamford, S., 1998. Flowering dynamics of *Orchis morio* L. and *Herminium monorchis* (L.) R. Br. at two sites in eastern England. Bot. J. Linn. Soc. 126, 39–48. https://doi.org/10.1111/j.1095-8339.1998.tb02514.x.
Zeppel, M.J.B., Wilks, J., Lewis, J.D., 2013. Impacts of extreme precipitation and seasonal changes in precipitation on plants. Biogeosci. Discuss. 10, 16645–16673. https://doi.org/10.5194/bgd-10-16645-2013.