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EPIPACTIS SPECIES AND THEIR HABITAT PREFERENCES IN THE WESTERN PART OF HUNGARY

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With 22 taxa reported from the country so far, *Epipactis* is the most species-rich orchid genus in Hungary. Many of them are rare, threatened species. To protect endangered species effectively, it is crucial to explore their ecology. Our work aimed to select and examine factors that are influencing the distribution of *Epipactis* species. Our data collection (2014–2018) was carried out in the Keszthely Hills, in the northeastern part of the Zala Hills and the Southern Bakony Mountains. We assigned ecologically relevant data from databases of local forestries, terrain models and geological maps to each occurrence. We examined the factors that result in the best differentiation between the studied species. At 1,261 localities, a total of 5,223 individuals of 15 taxa were found. We found three factors (tree species composition of the forest, genetic soil type, bedrock type) that significantly influenced the distribution of *Epipactis* species. Our results can help understand the distribution patterns of these species and allow for more effective, targeted protection of their potential habitats on a regional level.

Key words: bedrock, distribution, Orchidaceae, soil types, tree species

INTRODUCTION

Epipactis (Orchidaceae) is one of the most species-rich orchid genera of the north temperate zone. In Hungary, nearly one-third of the native orchid species belong to this group. The genus currently is in a state of rapid speciation, which could be explained by the evolutionary effect of their recent radiation from the Mediterranean towards the north after the last glaciation (Delforge 2006, Tranchida-Lombardo *et al.* 2011). The high rate of autogamy – which is a good strategy during rapid colonisation – in this genus might also be the consequence of this progress (Hollingsworth *et al.* 2006, Squirrell *et al.* 2002). *Epipactis* species are also adapted to clonal growth, which is also a beneficial trait in environments where pollination is limited by the scarcity of potential partners (Eckert 1999).

Due to this ongoing speciation, the genus' taxonomy is of high complexity, the number of accepted species greatly varies by authors and time as well (Delforge 1995, 2006, Molnár V. 2011).

Like every genus of Orchidaceae, *Epipactis* species also rely on symbiotic fungi during their germination, but often through their whole life cycle (Gonneau *et al.* 2014). Most of the known potential mycorrhizal partners of species in this genus are also ectomycorrhizal tree species (Schiebold *et al.* 2017). Although many *Epipactis* species have many potential fungi partners, this association is often highly specific. Many species have only one known mycorrhizal partner (Schiebold *et al.* 2017). Therefore, the distribution area of *Epipactis* species is limited not just by abiotic factors, but by the presence of their mycorrhizal partners, which is also affected by abiotic factors (Rasmussen and Whigham 1998, Taylor and Bruns 1999).

Partly due to their indirect dependence of particular tree species through their mycorrhizal partner, most *Epipactis* species are typically limited to only a few specific habitat types in their whole distribution area where the appropriate tree species occur (Hrivnák *et al.* 2014), in contrast with other orchid genera which often occur in diverse habitats at different parts of their distribution area (e.g., *Ophrys*, *Dactylorhiza*, *Orchis* spp.) (Abdullah 2018, Illyés *et al.* 2010). On the other hand, members of the *Epipactis* genus often considered pioneer species in general, since they frequently appear in secondary, disturbed habitats, like plantations or mines (Adamowski 2006, Jakubska-Busse *et al.* 2006, Rewicz *et al.* 2017, Shefferson *et al.* 2008, Süveges *et al.* 2020).

22 *Epipactis* species and subspecies were reported from Hungary according to recent publications, many of them only recently (Csábi and Halász 2016, Molnár V. 2011, Somlyay *et al.* 2016). Although in some cases their taxonomic rank is still disputed, we have some knowledge of the ecological preferences of the majority of these taxa. Most of these ecological data derives from descriptions attached to floristic data, though a few publications aimed to characterise and compare ecological preferences of certain *Epipactis* taxa (Hrivnák *et al.* 2014, Sulyok and Molnár V. 1998, Timpe and Mrkvicka 1996, Těšitelová *et al.* 2012) or orchid species in general (Djordjević *et al.* 2016).

The aim of our work was to determine if there are noticeable differences between ecological preferences of some *Epipactis* species in a relatively small area compared to their distribution area.

MATERIAL AND METHODS

Study areas

Data collection was carried out in six Natura 2000 sites in Western Hungary (Table 1, Fig. 1), as these areas represent well most natural habitats in this region.

The Keszthely Hills has two main parts with significant differences in their rock composition and habitat types, the Keszthely Plateau and the Tátika

Table 1
The sampled Natura 2000 sites and some details of the data collection.

Region	Site	Natura 2000 site code	Area (km^2)	Data collection
Keszthely Hills	Keszthelyi-hegység	HUBF20035	149.0	2014–2018
South Bakony Hills	Kab-hegy	HUBF20003	80.8	2017–2018
	Agár-tető	HUBF20004	51.4	2016–2018
Zala Hills	Zalaegerszegi Csácsi erdő	HUBF20053	11.3	2016
	Nagykapornaki erdő	HUBF20054	6.4	2016
	Remetekert	HUBF20055	9.7	2016

Group. The Keszthely Plateau is mainly composed of upper Triassic dolomite, on which rendzina, Eutric Cambisol and Lithic Leptosol are typical (Dövényi 2010). In this area, closed and open thermophilous oak woodlands and beech (*Fagus sylvatica*) forests are the most common (Bölöni and Bauer 2010).

The Tátika Group is of volcanic origin, mainly composed of basalt on which Eutric Cambisol and Haplic Luvisol are distinct soil types (Dövényi 2010). Besides beech forests, sessile oak (*Quecus petraea*) – hornbeam (*Carpinus betulus*) and lowland oak-hornbeam woodlands are the most common forest habitats in this area (Bölöni and Bauer 2010, Bölöni *et al.* 2011).

The two sites located in the Southern Bakony Hills (Kab-hegy, Agár-tető) are composed of volcanic rocks (mainly basalt) deposited on dolomite

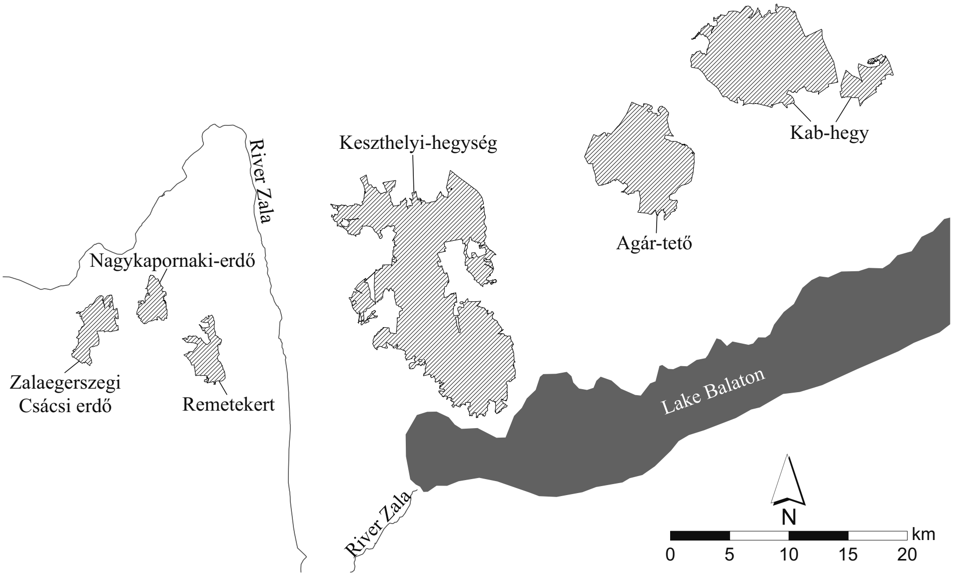

Fig. 1. Map of the study area and the sample sites

and limestone. Eutric Cambisol and Haplic Luvisol are the most frequent soil types in this area and rendzina are also prevalent (Dövényi 2010). The most common woodland habitats in this area are *Fagus sylvatica* and sessile oak-hornbeam woodlands with some uncharacteristic hardwood forests and plantations (Bölöni and Bauer 2010, Bölöni *et al.* 2011).

Zala Hills are composed of loam and loess deposited on Pannonic calcareous bedrock, on which Haplic Luvisol and Chromic Cambisol are typical (Dövényi 2010). The most common woodland habitats are sessile oak-hornbeam and beech woodlands, with many riverine ash-alder forests (Bölöni and Bauer 2010).

Methods

The data collection was done between 2014 and 2018; the position and the number of individuals occurring at one locality were recorded. The minimum distance between localities of one species was 100 m, all localities were documented once. If we found two or more *Epipactis* species on one point (which happened frequently), we recorded the localities separately, which means only one species belongs to each locality. We recorded 1261 localities altogether (Table 2).

We attempted to map the six sites near systematically by foot during fieldwork, which resulted in an 8.1 km/km^2 average sampling density (more than 2,500 km walk between May and September). In the study sites, the presence of 15 *Epipactis* species was detected (Table 2). We followed the nomenclature of Molnár V. (2011) and Somlyay *et al.* (2016).

We included in the statistical analysis those species which were found at least at eight localities. In that way, *E. pontica*, *E. muelleri* and *E. moravica* were excluded from the analysis. *E. palustris* was also excluded from the analysis given that it is not a forest species (unlike the other species studied), typically occurring in wet meadows and marshes.

To each of the localities, we have assigned geographical attributes [altitude (m), slope (°)], soil (soil type, bedrock) and forestry data [tree species composition, forest stand age and the canopy cover] based on the digital elevation model of the Department of Geodesy Remote Sensing and Land Offices, the geological map of the Geological Institute of Hungary and the databases of the three local forestries, Verga Ltd, Bakonyerdő Ltd and Zalaerdő Ltd.

In total, 34 tree species were found in forest subcompartments in which we recorded *Epipactis* species. We included the 11 most common tree species in the statistical analysis. Slavonian oak (*Quercus robur* subsp. *slavonica*) distinguished in the forestries' databases was merged into the pedunculate oak (*Quercus robur*), based on taxonomic consideration. The other 21 species, which were neglected in the statistical survey, were found in a few cases (< 10)

Table 2
The number of localities and the number of shoots (in parentheses) of the occurring species in the three regions. The species involved in the analysis are in bolditalics.

Species	Bakony Mts	Zala Hills	Keszthely Hills
Epipactis albensis Nováková et Rydlo	0	0	8 (31)
Epipactis atrorubens Hoffm. ex Besser	0	0	10 (217)
Epipactis helleborine (L.) Crantz	21 (123)	1 (2)	352 (1244)
Epipactis leptochila Godfery	0	16 (78)	42 (118)
Epipactis microphylla (Ehrh.) Sw.	13 (34)	5 (8)	71 (212)
Epipactis moravica P. Batoušek	0	0	7 (58)
Epipactis muelleri Godfery	0	0	7 (27)
Epipactis neglecta Kümpel	22 (41)	0	58 (235)
Epipactis nordeniorum Robatsch	44 (249)	33 (136)	57 (197)
Epipactis palustris (L.) Crantz	0	0	22 (116)
Epipactis peitzii H. Neumann et Wucherpf.	0	0	42 (163)
Epipactis pontica Taubenheim	0	0	5 (32)
Epipactis purpurata Sm.	23 (75)	162 (321)	9 (17)
Epipactis tallosii A. Molnár et Robatsch	0	0	86 (1047)
Epipactis voethii Robatsch	1 (3)	17 (35)	129 (407)

and/or in low proportion (< 5%) in the examined forest subcompartments. Their combined share in the tree canopy cover did not reach 3%.

Seven genetic soil types occurred in more than five cases; these were included in the analysis. Based on the geological map, a total of 32 bedrock types were assigned to *Epipactis* localities. For practical purposes, we classified these highly specific classes into seven main categories (dolomite, scree, loess, sediment, sand, basalt, marl).

To determine the extent of differences in each species' examined factors, in cases of each continuous variable (e.g., canopy closure and age of forest subcompartments), we used a single-variable analysis of variance (ANOVA). For each categorical variable (e.g., bedrock types, tree species composition of the forest subcompartments), we used multivariate logistic regression.

Spatial calculations and data management were done with ArcGIS 10.2 software. Analysing simultaneous responses of many species to several factors is often a task for ecologists that requires a multivariate analysis. The traditional approach is to use parametric multiple analysis of variance. For ecological applications, however, nonparametric approaches may be preferred. Several nonparametric multivariate methods for use in biology, ecology and the social sciences have been proposed. For these, a test statistic is obtained directly from distances calculated among sampling units where distance measure other than the Euclidean distance may be used.

Legendre and Anderson (1999) have proposed a method called distance-based redundancy analysis. It has the double advantage that it can be based on any distance measure of choice and it can provide a multivariate partitioning to test any individual term in a multifactorial design. This is a significant development, because it is precisely such designs that are most often used in ecological studies, due to the inclusion of several interacting factors.

The statistical analyses were performed using redundancy analysis (RDA) and variance partition (varpart). In the case of trees, we used their canopy cover percentages in the investigation. All analyses and the presentation of the results were done with R software version 3.5.3 (R Core Team 2019) and vegan package version 2.5-6 (Oksanen *et al.* 2019).

RESULTS

By redundancy analysis we found that although all examined factors had significant effect ($p > 0.01$ at 999 permutations) on occurrences of *Epipactis* species, particularly three factors (tree species composition of forest subcompartments, soil type and bedrock type) contributed to the explained variance with a total adjusted R^2 of 0.119 (Fig. 2). These three factors unique effects were comparable with the sum of variances explained together by one or two other explanatory variables.

The relationships between tree species composition and Epipactis *species*

Out of the examined factors, tree species composition of forest stands was the best predictor of occurrences of *Epipactis* species (RDA, adjusted $R^2 = 0.0667$, $p = 0.001$ at 999 permutations). Along the first RDA1 axis (Fig. 3) there is a distinct gradient with almost 2.5 times as much variance explained than by axis RDA2. *E. helleborine, E. muelleri* and *E. atrorubens* preferred *Quercus pubescens* and *Fraxinus ornus* or *Pinus*

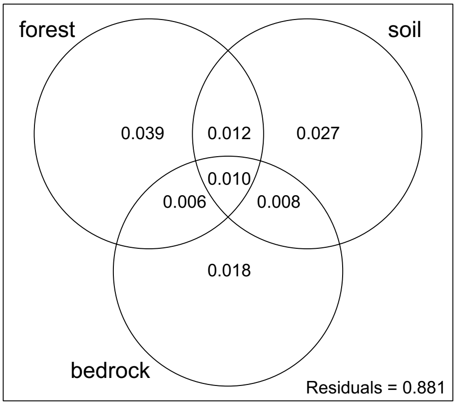

Fig. 2. Venn diagram showing the effects of tree species composition of forest subcompartments, soil type and bedrock type on *Epipactis* occurrences. The values indicate the adjusted R^2, as calculated from variation partitioning by RDA

nigra stands, while *E. purpurata, E. nordeniorum, E. leptochila* and *E. albensis* preferred *Fagus sylvatica*, *Carpinus betulus* and *Quercus robur* forest stands. Besides these two marked orientations, *E. microphylla* and *E. peitzii* preferred *Quercus cerris* and *E. nordeniorum* had preferences towards small-leaved lime. We found *E. tallosii* mainly in *Quercus robur* and *Carpinus betulus* forests, but the largest population was associated with a *Populus* stand mixed with *Quercus robur*. The other four species did not have defined preferences, but they disfavour thermophilous habitats with *Pinus nigra*, *Quercus pubescens* and *Fraxinus ornus*.

The relationships between soil types and Epipactis *species*

We also found soil type as a significant factor influencing *Epipactis* occurrences (RDA, adjusted $R^2 = 0.0566$, $p = 0.001$ at 999 permutations), but to a less extent than forest composition.

There were three distinct gradients (Fig. 4), with *E. purpurata* preferring Haplic Luvisols, *E. helleborine*, *E. peitzii* and *E atrorubens* preferring Rendzic Leptosols and *E. muelleri* was associated with Lithic Leptosols. Also, notable the preference of *E. nordeniorum* towards Eutric Leptosol.

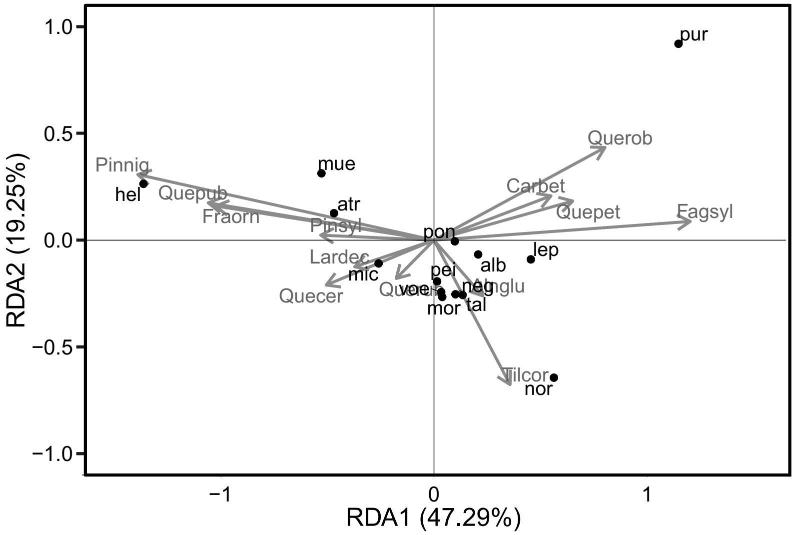

Fig. 3. Biplot of redundancy analysis (RDA) showing the correlations between tree- and *Epipactis* species. Tree species are represented by arrows and with grey text: Carbet, *Carpinus betulus*; Fagsyl, *Fagus sylvatica*; Fraorn, *Fraxinus ornus*; Lardec, *Larix decidua*; Quepet, *Quercus petraea*; Quepub, *Quercus pubescens*; Querob, *Quercus robur*; Querub, *Quercus rubra*; Pinnig, *Pinus nigra*; Pinsyl, *Pinus sylvestris*; tilcor, *Tilia cordata*. *Epipactis* species (represented by black circles): alb, *E. albensis*; atr, *E. atrorubens*; hel, *E. helleborine*; lep, *E. leptochila*; mic, *E. microphylla*; neg, *E. neglecta*; nor, *E. nordeniorum*; pei, *E. peitzii*; pur, *E. purpurata*; tal, *E. tallosii*; voe, *E. voethii*

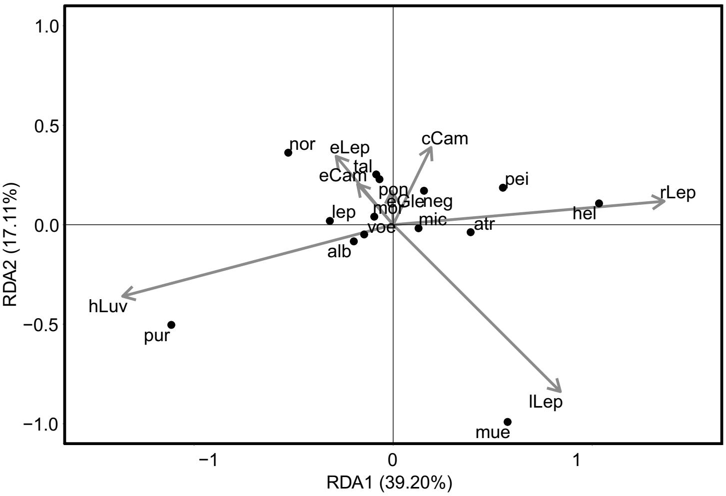

Fig. 4. Biplot of redundancy analysis (RDA) showing the correlations between *Epipactis* species and soil types on which they occurred. Arrows and grey text represent soil types: lLep: Lithic Leptosol; eLep: Eutric Leptosol; rLep: Rendzic Leptosol; hLuv: Haplic Luvisol; cCam: Chromic Cambisol; eCam: Eutric Cambisol; eGle: Eutric Gleysol. *Epipactis* species (represented by black circles): alb, *E. albensis*; atr, *E. atrorubens*; hel, *E. helleborine*; lep, *E. leptochila*; mic, *E. microphylla*; neg, *E. neglecta*; nor, *E. nordeniorum*; pei, *E. peitzii*; pur, *E. purpurata*; tal, *E. tallosii*; voe, *E. voethii*

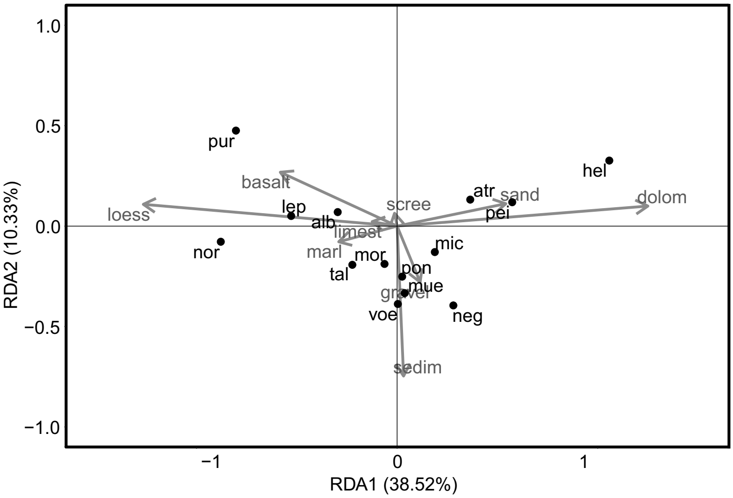

Fig. 5. Biplot of redundancy analysis (RDA) showing the correlations between *Epipactis* species and bedrock types on which they occurred. Bedrock types (represented by arrows and with grey text): dolom, dolomite; limest, limestone; sedim, sediment; *Epipactis* species (represented by black circles): alb, *E. albensis*; atr, *E. atrorubens*; hel, *E. helleborine*; lep, *E. leptochila*; mic, *E. microphylla*; neg, *E. neglecta*; nor, *E. nordeniorum*; pei, *E. peitzii*; pur, *E. purpurata*; tal, *E. tallosii*; voe, *E. voethii*

The relationships between bedrock types and Epipactis *species*

Bedrock type was a significant predictor as well (RDA, adjusted R^2 = 0.0418, p = 0.001 at 999 permutations), but it explained the least variation of the three factors described above.

In the case of bedrock type preferences, RDA analysis showed one strong gradient between loess and dolomite along with sand (x-axis explains four times as much variability as y-axis). There is a weaker gradient in the direction of sediments (Fig. 5). *E. atrorubens*, *E. helleborine* and *E. peitzii* had a marked preference towards sand and dolomite. *E. nordeniorum*, *E. purpurata*, *E. leptochila* and *E. albensis* preferred loess, although *E. albensis* in a less pronounced

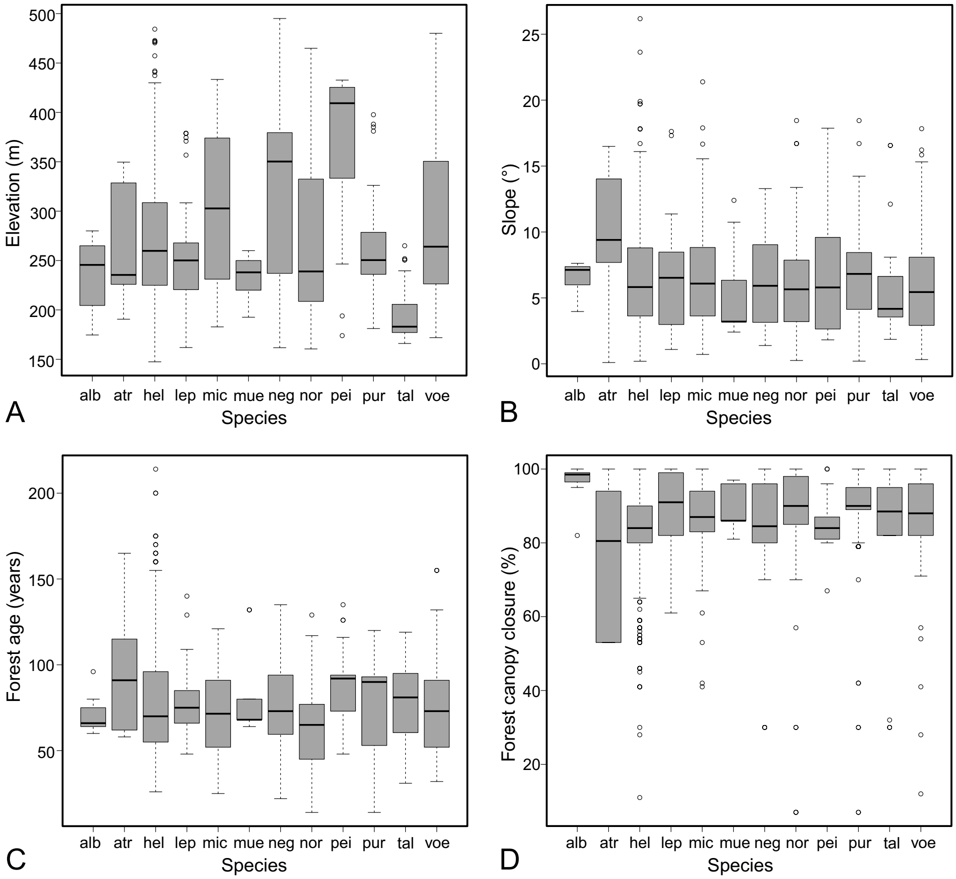

Fig. 6. Boxplots of elevation (a), slope (b), forest subcompartment age (c) and forest subcompartment average canopy closure (d) assigned to *Epipactis* spp. localities. *Epipactis* species: alb, *E. albensis*; atr, *E. atrorubens*; hel, *E. helleborine*; lep, *E. leptochila*; mic, *E. microphylla*; neg, *E. neglecta*; nor, *E. nordeniorum*; pei, *E. peitzii*; pur, *E. purpurata*; tal, *E. tallosii*; voe, *E. voethii*

way and *E. purpurata* had a distinct preference towards basalt also. The other seven species mostly preferred sediments.

Single-variable factors affecting the distribution of Epipactis *species*

Although we found that all examined single-variable factors had significant effect on distributions of *Epipactis* species, in most cases they behave similarly, only a few of them preferred considerably different conditions by some factors (Fig. 6).

By the elevation where *Epipactis* species occurred, there were several visible differences between some species (Fig. 6). Still, it had a less pronounced effect on their distribution (RDA, adjusted $R^2 = 0.0111$, $p = 0.001$ at 999 permutations). *E. peitzii*, *E. neglecta* and *E. microphylla* had a significant preference towards higher altitudes ($p = 0.001$ at 999 permutations), while *E. tallosii* preferred lower situated habitats. Age, canopy closure and slope had also significant effect, but only with adjusted R^2 of 0.0035; 0.0027 and 0.00084, respectively. All studied species occurred predominantly in forest stands of 50–80 years. Still, in some cases, significant number of occurrences were found in younger (e.g. *E. helleborine*, *E. microphylla*, *E. neglecta*, *E. nordeniorum*, *E. purpurata*) and much older (e.g. *E. atrorubens*, *E. helleborine*, *E. neglecta*, *E. voethii*) stands as well. Most examined *Epipactis* species occurred principally in stands with high (85–95%) canopy closure. Only *E. atrorubens* preferred forests with somewhat more open canopies as well. All species occurred mostly on slopes between 0° and 15° without many differences between the preferences of each species. Only *E. atrorubens* preferred more steep terrain.

DISCUSSION

The number of recorded localities showed remarkable differences in the three regions. The number of recorded species and individuals was significantly higher in the Keszthely Hills than in the other two areas. It is partly because the Keszthely Hills is the largest among the sample sites and hosts more habitat types, thus many species with different habitat preferences can find their favourable conditions in this relatively small area. Another factor that could influence this difference is that we collected data in the Keszthely Hills for the most extended period (Table 1) thus we had more chance finding populations that might appear dormant in years with less favourable conditions.

Dissimilarities between ratios of occurring *Epipactis* species on sites with different characteristics were observed. This phenomenon is most distinct in areas with diverse habitat types, as we experienced in Keszthely Hills, where besides *E. helleborine* and *E. voethii*, the two most common species, further 13 species were found. In Zala Hills *E. purpurata* was the most common species by far with many occurrences of *E. nordeniorum* and *E. leptochila* also, whereas *E. helleborine* was remarkably uncommon in the area. In Bakony Mts, we found the least number of species, of which *E. nordeniorum* was the most common. Out of the 15 species, only *E. nordeniorum* had a considerable number of occurrences in the study areas in all three regions, which is interesting, since according to present knowledge, this species has a small distribution area, confined to the Carpathian Basin and its immediate surroundings (Delforge 2006), particularly to Transdanubia (Molnár V. 2011).

In the case of *E. helleborine* we found a marked preference towards specific forests, bedrock and soil types as well, despite often being considered the most generalist species of the genus (Delforge 2006, Molnár V. 2011). However, there are large areas covered with *Fagus sylvatica* forests in all three regions, we found it frequently in thermophilous forests mainly composed of *Quercus pubescens* or *Pinus nigra*, which is uncommon among literature data (Aedo and Herrero 2005, Lorenz 2005).

Although previous publications indicate that *E. atrorubens* often occurs in *Fagus sylvatica* forests (Timpe 1995, Czarna *et al.* 2014) and this habitat type is common in our study area, we found this species predominantly in stands of *Pinus nigra* and *P. sylvestris*. Both tree species are non-native in the area, and they were used for afforestation of barren hilltops and southern hillsides in the region (Tamás 2003).

We found several *E. tallosii* occurrences in the Keszthely Hills site, mainly in humid stands of *Quercus robur* mixed with *Carpinus betulus*. Still, the largest population is partially situated in a canopy dominated by *Populus*. Since this habitat type is scarce in our study area (*Populus* spp. occurred only in two forest subcompartments with low proportions in the Keszthely Hills site), this might indicate a preference for *Populus* species. Lack of these habitat types not allowed to confirm it statistically, but it is supported by references in which *E. tallosii* were recorded from *Populus* stands and plantations (Molnár V. *et al.* 1998, Nagy 2015, Hadinec and Lustyk 2007).

We could find some significant differences between altitude preferences, although the highest and the lowest altitude in the study area had the difference of a mere 460 metres. Some of the studied species (e.g. *E. atrorubens*, *E. leptochila*, *E. microphylla*) occur in altitude ranges that are a multiple of this value (Delforge 2006), still we could indicate *E. peitzii*, *E. neglecta* and *E. microphylla* preferred higher altitudes and *E. tallosii* preferred lower situated habitats. The latter species often occurred in the vicinity of streams in the area, explaining their preference towards lower situated areas. This tendency towards riparian forest and lakeshores is also represented in literature data (Molnár V. 2011, Molnár V. *et al.* 1998).

Only one of the 11 studied species had pronounced slope preferences, *E. atrorubens* preferred more steep terrain. It might be influenced by the fact that most *Epipactis* occurrences were situated in valley bottoms or lower parts of valley sides. This factor's effect is significantly reduced mainly by the vegetation cover.

Although we found that tree species composition of forests had the strongest influence on species occurrences, other single factors also had a marked effect. In the case of *Epipactis purpurata* it especially preferred loamy soils and *E. atrorubens* preferred dolomite and sand as a bedrock.

Our study statistically confirms descriptions of most species habitat preferences by previous references (Delforge 2006, Molnár V. 2011) and its in good accordance with field experiences.

Since we used sources, which are available in the same standardised form for the whole country, we believe these results not only add some valuable information to the knowledge on the habitat preferences of these species in general, but they might help in localising potentially suitable habitats of *Epipactis* species. However, these results could be used with the most accuracy on a regional level.

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