

## Substrate associated biogeographical patterns in the north-western Pannonian forest-steppe

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**Abstract:** The north-western part of the Carpathian Basin is an important biogeographical crossroad. This transitional area between the forest-steppe biome of the Pannonian biogeographical region and the temperate forest biome hosts scattered patches of natural steppe embedded in forests, especially in rugged landscapes. The unique geographical position is reflected in the plant assemblages, which are composed of species of different origins, mainly central-European, continental, Mediterranean and sub-Mediterranean. We sampled sites with well-preserved forest-steppe vegetation on different substrates across this region. At each site, we sampled the vegetation in three habitats: steppe, forest and ecotone. We then attempted to disentangle the influence of geographical location, climate and substrate on the species composition of forest-steppe landscapes and the percentage of the species with a particular type of distribution. We found that substrate is the main factor determining species sorting. Substrate is also largely responsible for the percentage of species with particular types of distribution. While continental species are most frequent on loess, Mediterranean species are mainly found on andesite. Sub-Mediterranean species are most frequent on dolomite and rare on loess. The distributions of these species can be explained by the environmental conditions in the core of their native ranges. The complexity of the distribution patterns of species in the north-western Pannonian forest-steppe shown in this study should be considered in the discussion of the environmental history of the region and conservation planning.

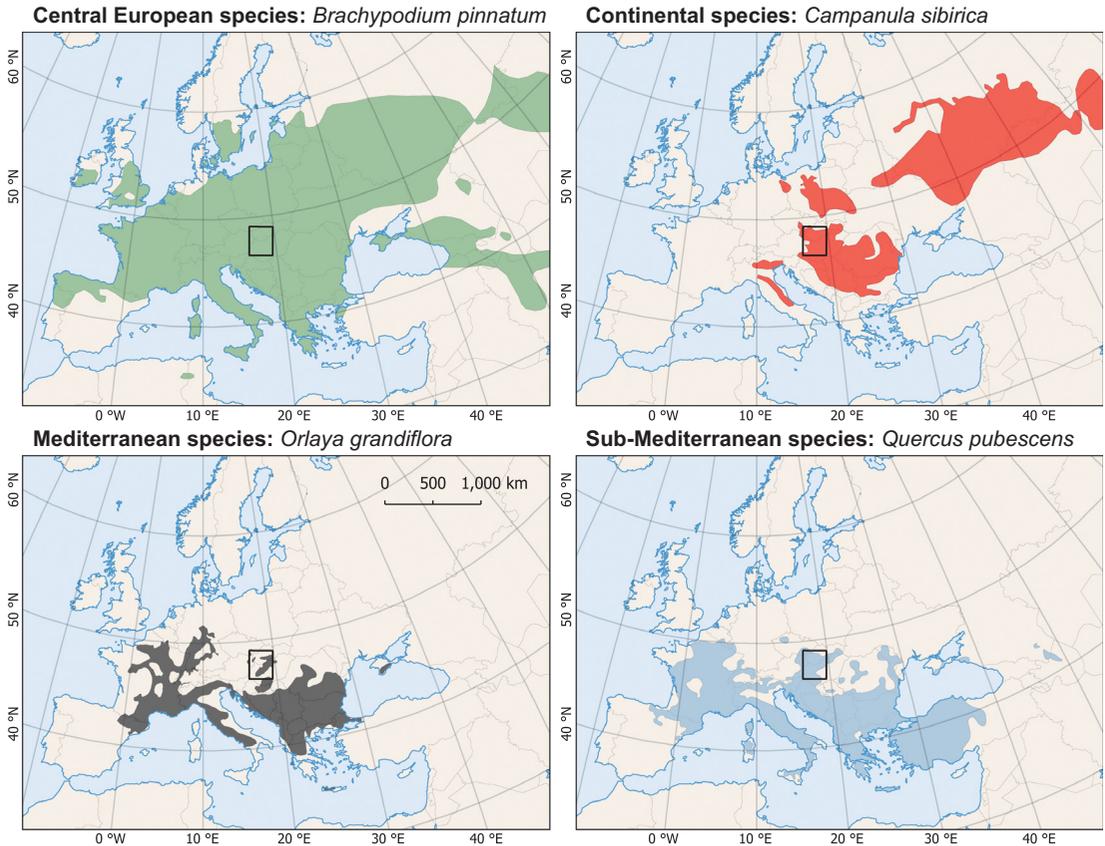
**Keywords:** Carpathian Basin, distribution limits, distribution range types, forest-steppe, habitat filtering, substrate, vegetation

### Introduction

The Eurasian forest-steppe biome extends over vast areas from central Europe through the Balkan Peninsula, Ukraine, southern Russia, the Caucasus, southern Siberia and northern Mongolia to northern China (Woodward 2008, Wesche & Treiber 2012, Erdős et al. 2018). It encompasses woodland-grassland mosaics on plains (e.g. Tölgyesi et al. 2018), exposed forest-steppes in rugged landscapes (e.g. Hais et al. 2016, Makunina

2016) and predominantly forested landscapes with isolated patches of steppe on south-facing slopes (e.g. Futák 1947, Illyés 2007). The forest-steppe biome lies between the biomes of temperate or boreal forest and steppe (Walter 1974). In more continental areas such as southern Siberia, the adjacent forest biome is mostly represented by open forests dominated by the conifers *Larix sibirica* and *Pinus sylvestris* or small-leaved deciduous trees such as *Betula pendula* and *Populus tremula* (Makunina 2016), while in the western parts, broad-leaved deciduous forest prevails, often dominated by *Quercus robur*, *Tilia cordata* and *Populus alba* (Walter 1974, Erdős et al. 2018). Within the forest-steppe biome, there are also various types of steppe, including meadow steppe, which occurs mainly on well-drained substrates on flatlands, and grass steppe, which occurs mainly on slopes (Dúbravková et al. 2010, Willner et al. 2017, Chytrý et al. 2022).

The westernmost limit to the distribution of forest-steppe is in central Europe, where this biome occurs in the Carpathian Basin (also called the Pannonian Basin) and smaller areas in northern and central Bohemia and central Germany (Meusel 1940, Korneck 1974, Chytrý 2012, Fekete et al. 2016, Erdős et al. 2018). In the Carpathian Basin, the forest-steppe biome is not connected with the steppe biome, as the basin is surrounded by mountain ranges and uplands (Fekete et al. 2016). Due to its isolation and various biogeographical influences from neighbouring areas, the Carpathian Basin can be considered to be a biogeographical crossroad where several contrasting biogeographical elements meet (Meusel & Jäger 1992, Chytrý 1995, Willner et al. 2021). Consequently, the forest-steppe mosaics in this area host four main biogeographical groups of plant species (Fig. 1): (i) Central-European species are the most common group in the study area. Their main distribution is in central Europe and only a few of them occur east of the Ural Mountains. They are mostly mesophilous and relatively nutrient-demanding herbaceous plants such as *Arrhenatherum elatius*, *Clinopodium vulgare* and *Melica transsylvanica*, and some species in this group are mesophilous trees such as *Fraxinus excelsior*, *Quercus petraea* and *Tilia platyphyllos* (Caudullo et al. 2017). (ii) The centre of the distribution of the continental species is in the steppe and forest-steppe zones of eastern Europe and western Asia (Berg et al. 2017). These species are mostly basiphilous, oligotrophic and light-demanding (e.g. *Adonis vernalis*, *Campanula sibirica*, *Festuca valesiaca* and *Stipa capillata*). Many of them are considered to be relics of Pleistocene steppes that once covered large parts of central Europe (Horsák et al. 2015, Janská et al. 2017). The persistence of open-landscape patches, especially in the mid-Holocene forest optimum, is considered a key factor in the survival of these species in central Europe (Magyari et al. 2010, Pokorný et al. 2015, Hájek et al. 2016, Novák et al. 2019). (iii) Mediterranean species are adapted to hot and dry summers and humid winters typical of the Mediterranean region (e.g. Volaire & Norton 2006, Fischer et al. 2020). This group includes mainly therophytes (e.g. *Cerastium brachypetalum*, *Bromus squarrosus* and *Orlaya grandiflora*), chamaephytes (e.g. *Fumana procumbens* and *Teucrium chamaedrys*) and shrubs (e.g. *Cotinus coggygria* and *Prunus mahaleb*). Many of these species are at the northern limit of their distribution within central Europe in the Carpathian Basin (Kaplan 2012). Several of them are recognized as archaeophytes (Pyšek et al. 2012), whose spread northwards was associated with the colonization of central Europe by agricultural societies (Fyfe et al. 2015, Giesecke et al. 2019). (iv) The centre of the distribution of sub-Mediterranean species is in the dry deciduous forests and grasslands in southern Europe (Meusel & Jäger 1992, Chytrý 1995). This group includes hemicytophytes such as *Galatella linoxyris*,



**Fig. 1.** Examples of species with the types of distributions considered in this study. The black rectangle represents the study area.

*Tanacetum corymbosum* and *Vincetoxicum hirundinaria*, trees and shrubs such as *Carpinus betulus*, *Cornus mas* and *Fraxinus ornus*, and geophytes, e.g. *Allium flavum* and *Anthericum ramosum*. This group also includes species with their core distributions in Mediterranean mountain ranges and the calcareous Alps, most notably *Clinopodium alpinum*, *Leontodon incanus* and *Teucrium montanum* (Meusel & Jäger 1992).

The co-occurrence of species with contrasting origins and distributions in forest-steppe mosaics has resulted in exceptional species diversity, which is recognized by vegetation ecologists and conservation biologists (e.g. Sádlo et al. 2007, Fekete et al. 2010, Habel et al. 2013, Le Roux et al. 2018). As a result, many types of grassland related to forest-steppe are protected at both national and international levels (Natura 2000, Emerald Network). Vegetation ecologists have made considerable efforts to study the pattern of diversity in central-European dry grasslands, often concluding that central-European steppes are related to zonal forest-steppes and steppes in Ukraine and south-western Russia (e.g. Dúbravková et al. 2010, Willner et al. 2017, 2019, Janišová et al. 2020) and several recent studies support earlier assumptions of the extensive distribution of these grasslands

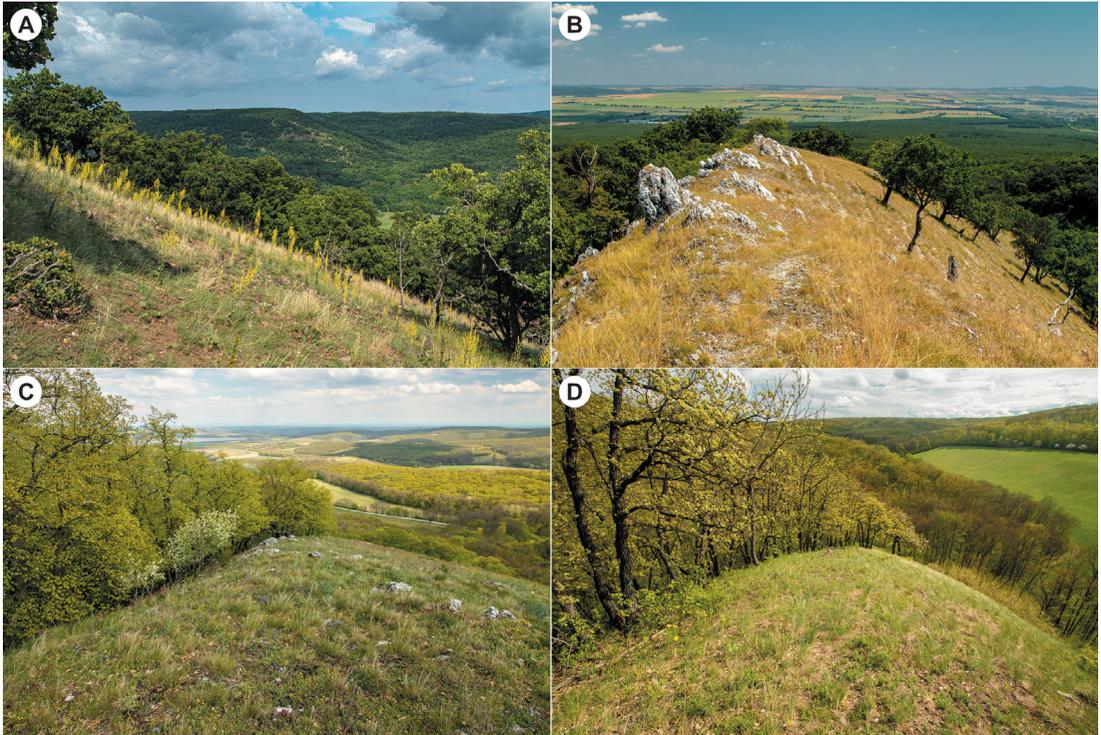
in the Pleistocene and Early Holocene (Kaplan 2012, Horsák et al. 2015, Chytrý et al. 2019, Willner et al. 2021). (Semi-)dry grasslands in forest-steppe have been further studied in order to disentangle their patterns of diversity and environmental relationships (e.g. Hegedúšová & Senko 2011, Dengler et al. 2014, Merunková et al. 2014, Roleček et al. 2014, 2019, Palpurina et al. 2017). However, the above studies focused on dry and semi-dry grasslands and neglected the considerable differences in species composition of other habitats in forest-steppe mosaics, i.e. ecotone and forest (compare Bátori et al. 2018, Erdős et al. 2020). There are several studies focusing on the gradient of species composition across all three major forest-steppe habitats, but they tend to focus on selected landscapes or compare a few areas (e.g. Dulamsuren et al. 2011, Erdős et al. 2013, 2014, Bátori et al. 2018, Tölgyesi et al. 2018; but see Erdős et al. 2019). Therefore, although we currently have a relatively good knowledge of the main gradients in species composition and underlying environmental factors occurring in different forest-steppe habitats in the Carpathian Basin, there is still no comprehensive analysis of the main compositional gradients across the forest-steppe mosaics in this region.

The aim of this paper is to examine the relative effects of edaphic, macroclimatic and geographical gradients on the composition of plant species in forest-steppe landscapes in the north-western Carpathian Basin. We asked (i) what are the effects of macroclimate, geographical location and substrate on species composition in forest-steppe and (ii) how do these factors influence the spectra of species with different types of distribution at individual forest-steppe sites?

## Methods

### *Study area*

We focused on the north-western part of the Carpathian Basin roughly between Lake Balaton (Hungary) and the cities of Brno (Czech Republic) and Veľký Krtíš (Slovakia). The study area includes the Hainburg Hills in Austria, the Pavlov Hills, the Podyjí National Park, the westernmost Carpathians and the Moravian Karst in the Czech Republic, the Little Carpathians, the Tematín Hills, the Strážov Mts, the Trábeč Mts, the Belá Hills, the Krupina Plateau and the Burda Hills in Slovakia, and the Börzsöny Mts, the Pilis Mts, the Vértes Mts and the Balaton Uplands in Hungary. In this area, we selected 32 sites with well-preserved exposure-related forest-steppe mosaics on different types of substrate (Fig. 2), including andesite, dolomite, limestone and loess. We attempted to sample forest-steppe on each substrate in as many different parts of the area studied as possible. However, the distribution of data from individual substrates differs in the final dataset due to differences in the geographic distribution of these substrates. For example, andesite bedrock is relatively common in southern Slovakia and northern Hungary from the Krupina Plain eastwards, while it is absent in other parts of the study area. Loess is restricted to the most continental lowland areas, where preserved forests are much rarer. Despite the wide distribution of loess steppes in Hungary (see Illyés 2007), we did not find a single site in north-western Hungary with natural forest suitable for our sampling.



**Fig. 2.** Forest-steppe mosaics on the four studied substrates: (A) andesite, Čierny hrad Hill northwest of Plášťovce, Krupina Plain, Slovakia; (B) dolomite, Nagy-Bükk Hill northwest of Csákvár, Vértes Mts, Hungary; (C) limestone, Děvín Hill north of Mikulov, Pavlov Hills, Moravia; (D) loess, Milovice slope south of Milovice, Pavlov Hills, Moravia. All photographs taken by Kryštof Chytrý.

### *Data collection*

The main criterion for selecting each site was the presence of (near-)natural forest and (near-)natural steppe free from recent (i.e. in the last 30 years; estimated in situ) disturbance such as removal of shrubs or young trees, which is a commonly used conservation measure in dry grasslands. We sampled five forest-steppe habitats at each site: (i) forest above the steppe patch, (ii) forest-steppe ecotone above the steppe patch, (iii) steppe, (iv) forest-steppe ecotone below the steppe patch and (v) forest below the steppe patch. We assume that these habitats are representative of the forest-steppe ecosystem and by sampling each of them in particular landscapes, we collected representative samples of this ecosystem. The steppe patch, i.e. the central part of each forest-steppe site, usually was on south-(west-)facing slopes. The forest above the steppe patch was mostly on a slope with the same inclination. However, at some sites, particularly on dolomitic bedrock, the ecotone was on a hilltop, so the forest was either on a flat surface or on a gentle north-facing slope. Forest on such sites was mostly transitional to a mesic type, especially in colder areas, where xeric types are more restricted. The forest below the steppe patch and its ecotone was always on a slope with the same or similar aspect as the steppe. At each site,

we subjectively selected representative places to sample these five forest-steppe habitats, mostly in parallel with the direction of the slope. Plot size was standardized at  $2.5 \times 4.0 \text{ m}^2$ , with the longer side aligned along the contour line. We chose a non-square plot size because of the linear nature of ecotones. We sampled vegetation using the Braun-Blanquet nine-degree cover-abundance scale (Westhoff & van der Maarel 1978). Bryophytes and lichens were not identified. For each vegetation plot, we estimated the covers of tree, shrub, herb and moss layers where present. At five sites, forests and ecotones below the steppe patch were absent or largely degraded; therefore, we sampled only the remaining three forest-steppe habitats.

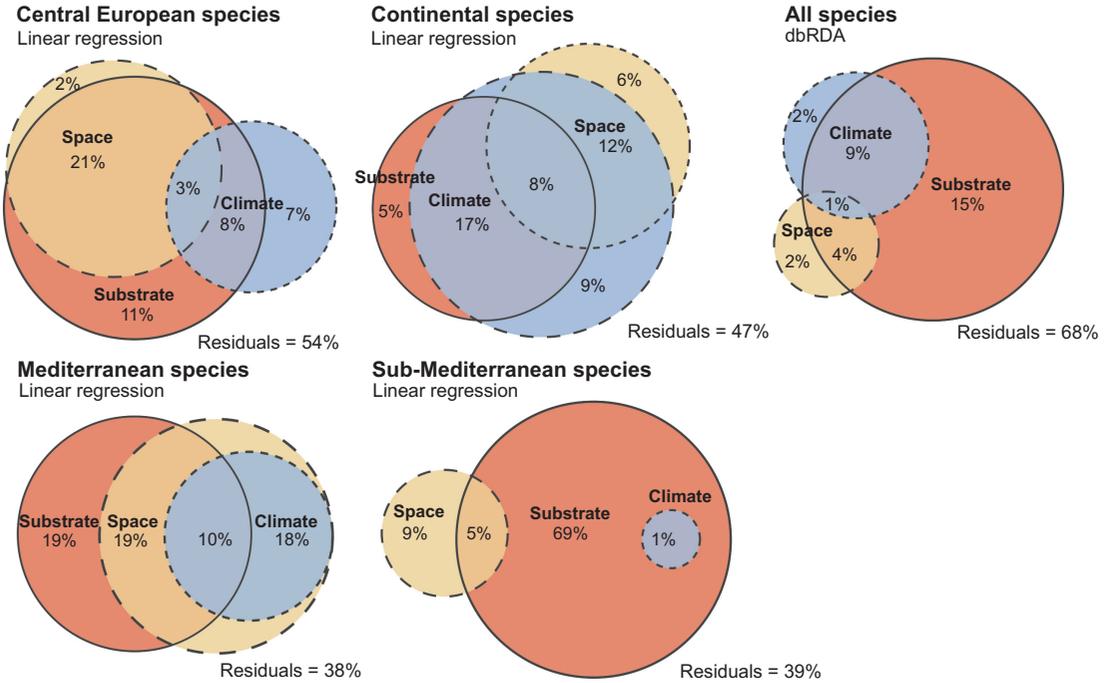
The dataset including species composition of vegetation plots, classification of species into types of distribution and site characteristics is stored in an open access online repository (<https://doi.org/10.5281/zenodo.4783984>). Data used for the analyses in this paper are marked there as “PART\_1”.

### *Data analysis*

We analysed only the herb layer, hence, we removed all trees and shrubs, except for juveniles. We performed all calculations in R (R Core Team 2021) using tidyverse (Wickham et al. 2019) and vegan (Oksanen et al. 2020) packages. Taxonomy and nomenclature of vascular plants follow the Euro+Med PlantBase (accessed February 2021). Taxa determined only at the genus level were not included in the dataset when they may have contained species already present in the dataset.

To examine the biogeographical patterns in the species composition of forest-steppe landscapes, we classified species into four groups based on their distributions. The classification is based on the distribution range types (Arealtypen) proposed by Meusel & Jäger (1992) and modified by Chytrý (1995): (i) central-European species (range types 8CE, 8sa and 8sc according to Chytrý 1995); (ii) continental species (type 4); (iii) sub-Mediterranean species (types 5, 6 and 8pa) and (iv) Mediterranean species (types 1 and 2). Species with other distribution range types were excluded from the analysis as well as species of non-European origin (although it concerned mostly rare species, the percentage of such excluded species was on average 28% of the total species diversity at a particular site). For each of these four groups, we calculated the percentage of species occurring at individual forest-steppe sites that we used for further analysis. We decided to use percentages (instead of absolute numbers) to eliminate the effect of variation in total species richness between sites, which is likely to be influenced by factors that were not considered in our study, such as the size of the patch of steppe and local topography. Moreover, the use of percentages also reduced the effect of the absence of the forest-steppe habitats located below the patch of steppe at some sites.

We used three groups of predictors to partition variation in species composition and the percentage of species with particular distributions (Borcard et al. 1992): (i) geographical space represented by latitude and longitude; (ii) macroclimate represented by mean annual temperature and annual precipitation (from Karger et al. 2017); and (iii) type of substrate (andesite, dolomite, limestone and loess). For partitioning variation in species composition, we used distance-based Redundancy Analysis (dbRDA) with the square-rooted Bray-Curtis dissimilarity matrix calculated from square-rooted percentage species cover values. The square-root of the dissimilarity matrix was used to make the dissimilar-

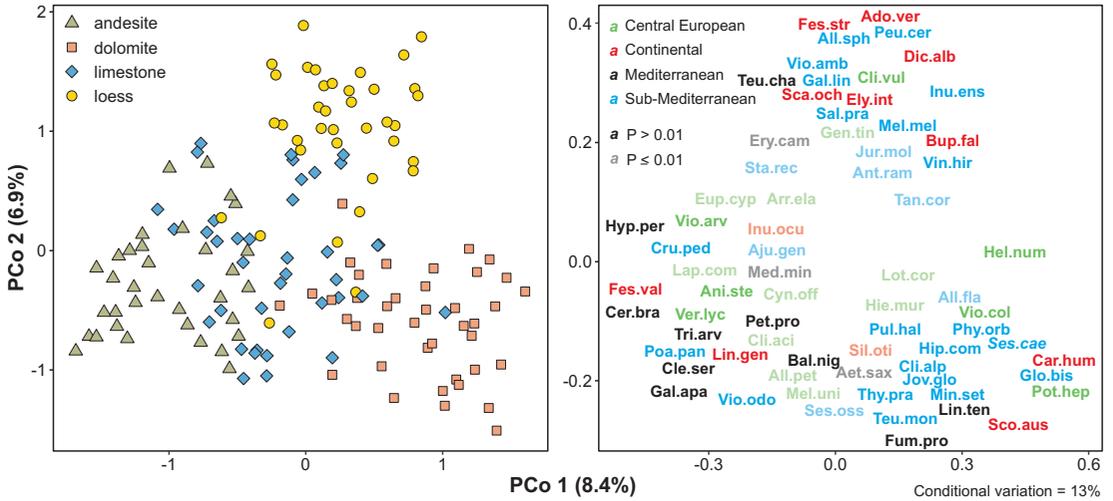


**Fig. 3.** Partitioning of variation in the percentages of species with different distributions and overall species composition explained by three groups of factors (substrate, space and macroclimate). The circle sizes are approximately proportional to the explained variation. Numbers are percentages of explained variation (adjusted  $R^2$ ) in linear regression and dbRDA models.

ities fully embeddable in Euclidean space (Legendre & Legendre 2012). We used habitat identity as a covariate to emphasize the biogeographical gradients in the studied forest-steppe mosaic. To partition variation in percentages of particular distributions, we used ordinary least squares regression. In these models, we allowed interactions between continuous variables. The amount of variation explained by the above groups of predictors was expressed in terms of the adjusted  $R^2$  (Peres-Neto et al. 2006). We plotted the partitioned variation in Venn diagrams using the R package *eulerr* (Larsson 2021).

We also modelled variation in species composition of forest-steppe mosaics. We used samples from each habitat and modelled them using partial Principal Coordinate Analysis (partial PCoA) based on square-rooted Bray-Curtis dissimilarity matrix calculated on square-rooted percentage covers. Again, we used habitat identity as a covariate. We plotted the results in two ordination diagrams, the first with sites and the second with species that occurred in more than three vegetation plots and showed significant fit to ordination axes ( $P$ -value < 0.05). Statistical significance was tested using a permutation test with 999 permutations.

Finally, we demonstrated the effects of the above predictors on the distribution of species with different types of distribution in three steps. First, we tested the affinity of each type of distribution to different types of substrate using the Wilcoxon test. Second, we plotted the same information in a scatterplot taking into consideration macroclimatic

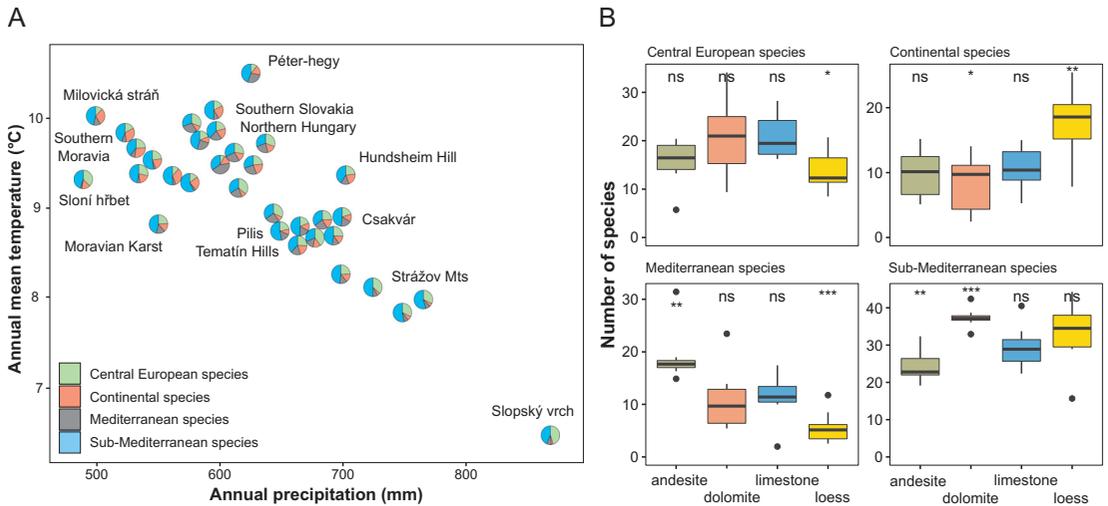


**Fig. 4.** Partial Principal Coordinate Analysis (PCoA) with habitat identity as a covariate. The second plot shows species that occurred in at least four plots and at the same time had a P-value  $\leq 0.05$  (determined using the envfit function; Oksanen et al. 2020). Species abbreviations refer to the first three letters of the genus name and the species epithet: Ado.ver: *Adonis vernalis*; Aet.sax: *Aethionema saxatile*; Aju.gen: *Ajuga genevensis*; All.fla: *Allium flavum*; All.pet: *Alliaria petiolata*; All.sph: *Allium sphaerocephalon*; Ani.ste: *Anisantha sterilis*; Ant.ram: *Anthericum ramosum*; Arr.ela: *Arrhenatherum elatius*; Bal.nig: *Ballota nigra*; Bup.fal: *Bupleurum falcatum*; Car.hum: *Carex humilis*; Cer.bra: *Cerastium brachypetalum*; Cle.ser: *Cleistogenes serotina*; Cli.aci: *Clinopodium acinos*; Cli.alp: *Clinopodium alpinum*; Cli.vul: *Clinopodium vulgare*; Cru.ped: *Cruciata pedemontana*; Cyn.off: *Cynoglossum officinale*; Dic.alb: *Dictamnus albus*; Ely.int: *Elytrigia intermedia*; Ery.cam: *Eryngium campestre*; Eup.cyp: *Euphorbia cyparissias*; Fes.str: *Festuca stricta* subsp. *sulcata*; Fes.val: *Festuca valesiaca*; Fum.pro: *Fumana procumbens*; Gal.apa: *Galium aparine*; Gal.lin: *Galatella linoisyris*; Gen.tin: *Genista tinctoria*; Glo.bis: *Globularia bisnagarica*; Hel.num: *Helianthemum nummularium*; Hie.mur: *Hieracium murorum*; Hip.com: *Hippocrepis comosa*; Hyp.per: *Hypericum perforatum*; Inu.ens: *Inula ensifolia*; Inu.ocu: *Inula oculus-christi*; Jov.glo: *Jovibarna globifera*; Jur.mol: *Jurinea mollis*; Lap.com: *Lapsana communis*; Lin.gen: *Linaria genistifolia*; Lin.ten: *Linum tenuissimum*; Lot.cor: *Lotus corniculatus*; Med.min: *Medicago minima*; Mel.mel: *Melittis melissophyllum*; Mel.uni: *Melica uniflora*; Min.set: *Minuartia setacea*; Pet.pro: *Petrorhagia prolifera*; Peu.cer: *Peucedanum cervaria*; Phy.orb: *Phyteum orbiculare*; Poa.pan: *Poa pannonica*; Pot.hep: *Potentilla heptaphylla*; Pul.hal: *Pulsatilla halleri* subsp. *styriaca*; Sal.pra: *Salvia pratensis*; Sca.och: *Scabiosa ochroleuca*; Sco.aus: *Scorzonera austriaca*; Ses.cae: *Sesleria caerulea*; Ses.oss: *Seseli osseum*; Sil.oti: *Silene otites*; Sta.rec: *Stachys recta*; Tan.cor: *Tanacetum corymbosum*; Teu.cha: *Teucrium chamaedrys*; Teu.mon: *Teucrium montanum*; Thy.pra: *Thymu praecox*; Tri.arv: *Trifolium arvense*; Ver.lyc: *Verbascum lychnitis*; Vin.hir: *Vincetoxicum hirsutiflorum*; Vio.amb: *Viola ambigua*; Vio.arv: *Viola arvensis*; Vio.col: *Viola collina* and *Viola odorata*.

space, i.e. annual precipitation and mean annual temperature. Third, we displayed using maps the percentage of species with specific distributions.

## Results

Variation partitioning (Fig. 3) showed that the variability in species composition of central-European forest-steppe vegetation depends largely on substrate (pure effect 15%, adjusted  $R^2$ ,  $df = 3$ ). A considerable part of the variation explained by substrate is shared

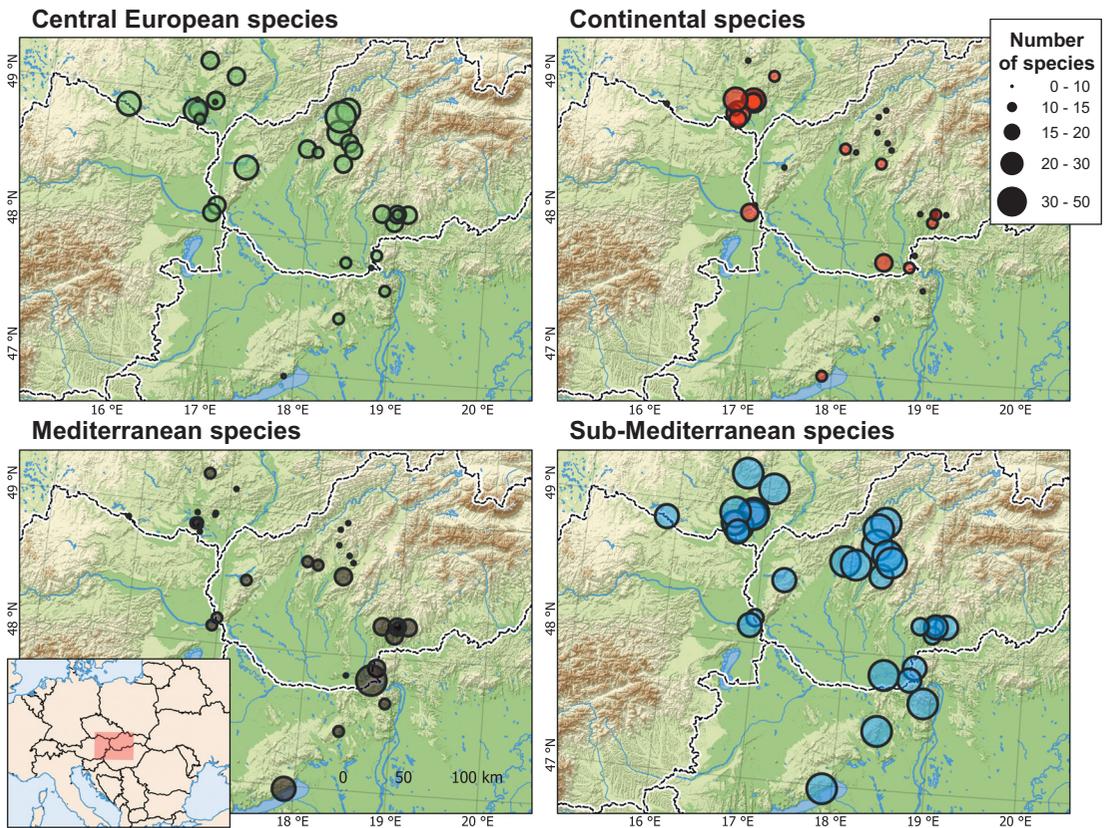


**Fig. 5.** (A) The percentage of the types of distribution within ecological (climatic) space. Pie charts are of equal size and were manually shifted to reduce overlap. Labels were placed manually to aid the interpretation. The pie charts were drawn using the R package *scatterpie* (Yu 2021). (B) Relationship of distributions to different substrates. We used the Wilcoxon test to test for differences from the overall mean. Asterisks indicate significance levels (\*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , \*  $P < 0.05$ ). We used the R package *ggpubr* (Kassambara 2020).

with either macroclimate (i.e. annual precipitation and mean annual temperature; 9%) or geographical location (i.e. coordinates; 4%). The effect of macroclimate is stronger than the effect of geographical location, while the overlap of these two factors is relatively small. The unsupervised ordination model (partial PCoA; Fig. 4) supported the assumption that substrate is the most important filter for species composition at the landscape scale. On the first two axes, the model captured 15% of the total variation, most of which could be explained by variation in the substrate. The first ordination axis reflected the distinction between andesite and dolomite, and the second axis mainly separated loess sites from other types of substrate. Limestone forest-steppes occupied an intermediate position, but were more separated from the other sites on other ordination axes (not shown).

Consistent with the analysis of species composition, the distribution of species with different types of distribution was mainly determined by substrate (Fig. 5B). However, the contributions of macroclimate (Fig. 5A) and geographical location (Fig. 6) were also pronounced and depended on the type of distribution.

(i) Central-European species are relatively common in the dataset, especially on limestone and dolomite. In addition, they tend to be more frequent in the northern part of the study area and decrease along the climatic gradient towards the south (Fig. 5A). This is well seen, for example, in their decline from the wetter dolomite sites in the north of the Strážov Mts (Slopeský vrch and Košecké Podhradie) towards the Tematín Hills located further to the south. Moreover, there are almost no central-European species in the forest-steppe landscapes of the Transdanubian Mts, which are separated from the former sites by the Little Hungarian Plain. A similar gradient occurs on andesite between the more mesic Krupina Plain and the drier Börzsöny and Buda Mts. Central-European species are most abundant in the mesic parts of the Strážov Mts and also on limestone substrates in



**Fig. 6.** The effect of space on the distribution of species with different types of distribution. Unlike in the previous plot, the size of the data points reflects the number of species in each group.

southern Moravia. However, loess sites in the same region host significantly fewer species of this group. The variation partitioning suggests that their distribution is mainly determined by the spatially structured influence of the substrate.

(ii) Continental species are rare in the dataset. They are most abundant on loess (Fig. 5B) in southern Moravia, which is the driest part of the study area (Karger et al. 2017). The number of continental species decreases towards the south (Fig. 6), where the climate becomes warmer and somewhat wetter, and towards high altitudes. The single loess site in southern Slovakia still hosts a relatively high number of continental species, while surrounding sites on other bedrocks host much fewer. Continental species are the least common in the areas with high precipitation, such as the Moravian Karst, the Podyjí National Park and the northern part of the Strážov Hills. They are also rather rare in the Transdanubian Mts. The variation partitioning showed that the spatially structured effects of substrate and climate are the most important for their distribution.

(iii) Mediterranean species show a clear pattern of a northward decline in their frequency (Fig. 6). The northward direction is related both to an increase in spatial distance and decrease in climatic similarity with the areas of their core distribution. While

Mediterranean species are relatively common in the southern part of the study area (north-western Hungary and southern Slovakia), they are much rarer in the northern part. They are especially rare in the northern part of the Strážov Mts and in southern Moravia, especially on loess. They seem to avoid loess as evidenced by their exceptionally low frequency at the loess sites in the Belá Hills in southern Slovakia, which sharply contrasts with their high incidence on other substrates at nearby sites (Fig. 6). Another deviation from the climate-space-driven gradient in their abundance seems to occur on andesite, where they are more common (Fig. 5B). They reach their highest numbers on andesite in relatively dry areas such as the Börzsöny and the Buda Mts. In general, they seem to avoid the driest areas (Fig. 5A), though, in this case our results can be misleading due to the predominance of loess in the driest north-western part of the study area (southern Moravia). Mediterranean species also avoid areas with high precipitation such as the Podyjí National Park and the northern part of the Strážov Mts. The variation partitioning showed that the highest percentage of variation is explained by substrate, but the contribution of space and macroclimate is also important. The total percentage of explained variation is relatively high.

(iv) Sub-Mediterranean species are the most common in the dataset. They are most abundant on dolomite and least abundant on andesite (Fig. 5B). They are well represented in the dolomitic Tematín Hills and the Strážov Mts, but also in southern Moravia on loess and in the Transdanubian Mts on both limestone and dolomite. Their number does not show a strong pattern of variation in geographic space. Variation partitioning showed a high importance of substrate, which is probably caused only by their lower frequency on andesite, a small contribution of space and almost no contribution of macroclimate.

## Discussion

The species composition of forest-steppe mosaics in the north-western part of the Carpathian Basin is mainly determined by the substrate, as shown by both the partitioning of variation in species composition (Fig. 3) and the partial PCoA (Fig. 4). The effect of macroclimate was slightly stronger than that of the geographical location and both were mostly shared with the effect of substrate. Further insight into the dynamics of species composition of forest-steppe mosaics in the study area comes from the partitioning of species composition into types of distributions. The turnover in types of distributions is influenced by all the mentioned factors, i.e. substrate, macroclimate and geographical location, although the factors vary in importance among groups of species with similar distributions.

### *Ecological niche conservatism and the limits on distribution*

The north-western part of the Carpathian Basin is characterized by the coexistence of species with contrasting origins. Central-European species become rarer towards the drier inner parts of the basin. The north-western part of the basin is also the area where many continental species reach the westernmost limit to their distribution and many sub-Mediterranean, and even more Mediterranean species reach their northern limit (Fig. 1). Our results indicate that the coexistence of these species is favoured by the environmental diversity in this region, especially its geological diversity. Some species are simply more

abundant on certain types of bedrock and reach the limits of their distribution on these particular bedrocks. Usually, these substrates are characteristic of the core part of the distributions of such species. This biogeographical pattern is described as a “Law of relative site constancy” (in German: Gesetz der relativen Standortkonstanz; Walter & Walter 1953), however, the empirical evidence for it is still rare (e.g. Nimis & Bolognini 1993, Chytrý 1995, Duchoslav 2009). In our dataset, we detected this pattern in several cases. It clearly applies to continental species, which are remarkably associated with loess sites (Důbravková et al. 2010). Loess is common in present-day steppe and forest-steppe biomes (Haase et al. 2007). In the Pleistocene and Early Holocene, it also covered vast areas of central Europe, but by the Middle Holocene, many loess areas were covered by forest (Ložek 2007). Consequently, open dry grasslands on loess became restricted to the driest areas, where forest occurred for a short time or was entirely absent in the Holocene. Another example, although possibly less obvious, is the relation of the Mediterranean species to andesite. So far, we have no definitive explanation for this phenomenon, nevertheless, it is probably related to the physical properties of volcanic soils. They are composed of fine-grained sandy material with a high proportion of stones and therefore tend to dry out in summer. The physiological dryness of such soils could be enhanced by the dark (almost black) colour of andesite, especially in contrast to white limestone and dolomite or yellowish-brownish loess. A substrate that often dries out in summer is not preferred by perennial plants (Hroudová & Prach 1986, Fischer et al. 2020). Therefore, grasslands on andesite are sparse and have many open patches required by annuals (Mikyška 1933, Klika 1938, Májovský & Jurko 1956), similar to open habitats in the Mediterranean. Annual plants are further favoured by early spring warming on rocky substrates.

### *Many species, many biogeographical stories*

Distinct patterns in the distributions of species indicate that species with a particular distribution type have a shared history, which has implications for the interpretation of past vegetation processes. For example, the decline of central-European species towards the inner parts of the Carpathian Basin supports the assumption that the basin harbours a different biome (forest-steppe) than the rest of central Europe, which corresponds to the temperate forest biome (Fekete et al. 2010, Erdős et al. 2018). In the study area, the decline of central-European species is associated with the increase in Mediterranean species. It is reported that the Pannonian forest-steppe is indeed influenced by the Mediterranean flora, especially along its western margin (e.g. Jakucs 1961, Fekete et al. 2014). In contrast, close to the centre of the Carpathian Basin, Fekete et al. (2010) report a nested pattern of shared decline of both steppe and forest species, which they interpret as a consequence of the lack of the zonal steppe in the Carpathian Basin because of the environmental history of the region. The history of steppe species in the Carpathian Basin is a controversial topic that has been extensively debated in the last decades. Some researchers suggest that the steppe flora went extinct in central Europe in the Middle Holocene, and later recolonized the area from refugia in southern and eastern Europe with the help of agricultural societies (Litt 1992, Lang 1994, Rybníček & Rybníčková 1994). While this theory has been abandoned by most current researchers, other interpretations suggest a Holocene continuum of steppe species in central Europe (Magyari et al. 2010, Kuneš et

al. 2015, Pokorný et al. 2015, Kirschner et al. 2020, Willner et al. 2021). Steppe species and plant communities could have survived on rocky outcrops and easily erodible soils (Zólyomi 1942, 1953), on sites with a suitable microclimate (Chytrý et al. 2022) and in areas that were kept free of forest by prehistoric agricultural societies (Gradmann 1933, Kuneš et al. 2008, Novák et al. 2019) or wild herbivores and natural fires (Walter 1974, Vera 2000).

Based on the present-day patterns in the distributions of species with different ranges, we suggest that all the above interpretations might be relevant in certain cases. Sub-Mediterranean species could have survived locally on rocky outcrops or on dolomitic soils, where they are currently most abundant, and later spread into the lowlands. Moreover, wetter dolomitic sites located at high altitudes host a group of sub-Mediterranean species otherwise common in the calcareous Alps and Mediterranean mountains, which do not occur elsewhere in the area studied (see also Sillinger 1930, Duchoň 2013). In contrast, continental species might not follow this path because at present they are almost absent from such sites. However, their isolation in the north-western part of the study area indicates that they most likely survived *in situ* there, probably supported by the activities of prehistoric agricultural societies (Kuneš et al. 2008, Novák et al. 2019). Forest-steppe sites on loess are characterized by smooth transitions between forest and grassland with a low turnover in species composition (Chytrý 2021), which might be related to the high tolerance of their species composition to overgrowing by shrubs and partly also by forest (Teleki et al. 2020). This also supports the hypothesis of their Holocene persistence in the study area. Finally, some Mediterranean species may have survived the precipitation-rich period in the Middle Holocene, perhaps on andesite sites, where they are most abundant today (see also Míkyška 1933, Májovský & Jurko 1956). Some Mediterranean species may also have spread from southern Europe (or at least from the inner parts of the Carpathian Basin), which would explain their northward decline.

Overall, our analysis demonstrates that the north-western Pannonian forest-steppe is a complex biogeographical phenomenon, which results from an interplay of past colonization, persistence in refugia and contrasting affinities of individual forest-steppe species for particular substrates and climates.

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## Podloží podmiňuje biogeografickou patrnost v lesostepích severozápadní Panonie

Severozápadní Panonie je významnou biogeografickou křižovatkou. Na pomezí biomu lesostepí a listnatého opadavého lesa zde převážně v členitých krajinách nalezneme roztroušené stepní enklávy odpovídající reliktním dřívě širěji rozšířené lesostepi. Biogeografický význam reliktních lesostepních krajin a potažmo celé této oblasti se odráží ve společenstvech rostlin, ve kterých se ve zdejších lesostepích objevují druhy s různou historií a různými typy rozšíření (areálytypy). Především jde o druhy středoevropské, kontinentální, mediteránní a submediteránní. Během našeho výzkumu jsme cíleně vyhledávali zachovalé lesostepní krajiny, abychom v nich zapsali fytoocenologické snímky v pěti předem vytipovaných biotopech: les a ekoton nad stepní enklávou, step a ekoton a les pod stepní enklávou. Celkem jsme tímto způsobem provedli terénní výzkum na 32 lokalitách v prostoru přibližně mezi Brnem, Velkým Krtářem a Balatonem. Následně jsme data o rozšíření druhů korelovali s typem podloží, geografickou lokací a makroklimatem. Tuto analýzu jsme provedli jak pro celkové druhové složení pomocí mnohorozměrných metod, tak i pro poměrné zastoupení druhů náležících k jednotlivým areálytypům. Zjistili jsme, že nejvýznamnějším faktorem předurčujícím druhové složení lesostepních krajin je substrát. Ten je především do velké míry zodpovědný za poměrné zastoupení druhů s jednotlivými areálytypy. Zatímco kontinentální druhy se nejčastěji vyskytují na spraších, mediteránní druhy byly nejvíce zastoupené na andezitech. Submediteránní druhy byly hojně na dolomitech, naopak na spraši byly poměrně vzácné. Rozšíření druhů náležících do jednotlivých areálytypů můžeme vysvětlit podmínkami prostředí panujícími v jádru areálu jejich přirozeného rozšíření. Nakonec konstatujeme, že komplexita patrností, jež formují vegetaci lesostepí v severozápadní Panonii, by měla být zohledněna v diskusi o historii zdejších krajin a v aplikované ochraně přírody.

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