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RESEARCH ARTICLE

Ecotones in Central European forest–steppe: Edge effect occurs on hard rocks but not on loess

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Abstract

Aims: We asked how geological substrate affects the distribution of plant species between forest interiors, forest edges, and steppe patches in the forest–steppe landscapes. Specifically, we sought for the presence of the edge effect at the forest–grassland transitions on different substrates.

Location: Austria, Czech Republic, Hungary, Slovakia and western Ukraine.

Methods: We recorded the occurrence of vascular plant species in forest interiors, at forest edges and in steppe patches on 40 forest–steppe sites located on four substrates (andesite, dolomite, limestone and loess). We compared the distribution of species diversity, beta diversity (using multivariate analysis), the number of shared species between habitats and the estimation of vegetation biomass among forest-steppe habitats on different substrates.

Results: The edge effect was observed on hard rocks, while it was absent on loess, where the ecotone species richness was intermediate between that of forest and steppe. Loess sites also had the lowest species turnover between forest and steppe and the lowest number of edge specialists.

Conclusions: Substrate has a strong effect on the formation of forest–steppe mosaics. It shapes the assembly rules and plant community diversity within individual habitat mosaics. Plant communities on each substrate can respond differently to changing climate. The strong assembly rules on hard rocks may be more likely to result in species loss than on loess or similar soft sediments, where a larger number of species find their optimum in more than one forest–steppe habitat.

KEYWORDS
ecotone, edge-effect, forest-steppe, habitat mosaic, substrate, vegetation

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1 | INTRODUCTION

The transition between forest and steppe biomes on continental scale is usually caused by a continuous macroclimatic gradient. However, landscapes in the transitional areas do not consist of physiognomically intermediate vegetation types, but of mosaics of forest and steppe patches (Erdős et al., 2018; Chytrý et al., 2022a). The mosaic nature of such landscapes has many consequences for biodiversity, species distribution, land use and conservation planning (Erdős et al., 2014, 2018). Therefore, the Eurasian forest–steppe is sometimes recognized as a distinct biome (Erdős et al., 2018).

Within Eurasia, forest–steppe has an extensive distribution with the westernmost large exclave in the Carpathian (=Pannonian) Basin in Central Europe (Chytrý, 2012; Fekete et al., 2016; Erdős et al., 2018; Chytrý et al., 2022a). Further west, forest–steppe occurs in isolated areas in the lee of mountain ranges in northern Bohemia, central Germany and in dry inner-Alpine valleys. In the western part of the Carpathian Basin and in the other dry areas mentioned above, forest–steppe consists of steppe patches embedded in broad-leaved deciduous forests. These landscapes are characterized by environmental contrasts between their main habitat types, forest and steppe (Dierschke, 1974; Burgess & Sharpe, 1981; Faliński, 1986). While forests generally create a relatively stable environment where canopy shading reduces solar radiation and buffers climatic extremes (De Frenne et al., 2019), steppes face a dry and unstable macroclimate that is harsh for plant growth (Jakucs, 1972; Slavíková, 1983). This contrast leads to pronounced species turnover between forest and steppe (Dierschke, 1974; Łuczaj & Sadowska, 1997; Erdős et al., 2014). Indeed, neither closed forest nor extensive steppe are a suitable environment for all plant species as both represent a kind of 'extreme' environment. However, the boundary between the two, the ecotone, may represent intermediate conditions. The forest–steppe ecotone is partially shaded, which limits the adverse effects of direct sunlight, but still ensures sufficient light for species that are generally considered light-demanding to thrive (see Roleček et al., 2017). Partial shading and lower wind speeds also buffer climatic extremes and reduce evaporation and transpiration, which promote water retention (De Frenne et al., 2019; Süle et al., 2020). Leaf litter is partially blown away from ecotones, resulting in less nutrient enrichment than in the forest interior (Gonschorrek, 1977). In summary, ecotones mitigate some unfavourable environmental conditions of steppe and forest and therefore support the coexistence of species from both habitats; in some cases, they also contain species restricted to them (Erdős et al., 2014, 2019). Consequently, the ecotone can be more species-rich than either of the adjacent habitats (Leopold, 1933; Odum, 1971; Risser, 1995; Kent et al., 1997; Erdős et al., 2014). This increase in species richness in ecotones compared to adjacent habitats is called the positive edge effect (Łuczaj & Sadowska, 1997).

On a broad scale, the distribution and proportion of individual habitat patches in forest–steppe mosaics is determined mainly by macroclimate (Hais et al., 2016; Chytrý et al., 2022a). On a finer scale, it is determined by the distribution of plant-available moisture (Liu et al., 2012; Anenkhonov et al., 2015; Fajmonová et al., 2020) and community-level feedback loops (Wilson & Agnew, 1992; Agnew et al., 1993; Alftine & Malanson, 2004; Wiegand et al., 2006). Moisture availability is influenced by an intricate combination of interdependent factors that include variation in microclimate and soil properties. In hilly landscapes of the northern hemisphere, north-facing slopes tend to have more stable microclimate and moisture availability than south-facing slopes (Slavíková, 1983; Rorison et al., 1986; Bennie et al., 2008). As a result, steppe occurs preferentially on south-facing slopes, where it occupies increasingly larger areas towards drier macroclimates, whereas forest is restricted to north-facing slopes (Hais et al., 2016; Chytrý et al., 2022a). The availability of moisture to plants depends largely on its retention time in the soil, which in turn reflects the physical properties of the soil. In the Central European climate (i.e., annual mean temperatures of about 6–12 °C, annual precipitation of about 450–1000 mm, temperature and precipitation peak in summer and cold winters with frost; Karger et al., 2017), fine-grained soils promote water retention, are wet longer and favour vegetation succession. In contrast, coarse-grained soils, such as those on sand or weathered dolomite, tend to lose water due to better draining, creating an unstable environment. Vegetation on such soils is stressed by irregular drought events that can suppress vegetation succession (Hroudová & Prach, 1986; Fischer et al., 2020). Although the effects of substrate on community assembly have been studied by different research teams (e.g., Luzuriaga et al., 2015; Chytrý et al., 2022b), it is poorly understood how substrate affects habitat distribution and various components of species diversity in mosaic landscapes of forests and grasslands.

In this study, we attempt to clarify how substrate affects the structure of Central European forest–steppe mosaics, especially the nature of ecotones between forest and steppe habitats. We selected 40 natural forest–steppe sites in hilly landscapes on andesite, dolomite, limestone and loess, which are among the most common substrates for forest–steppe in this region (Mezősi, 2017). In the lowland landscapes of the study area, (near-)natural forest–steppe also occurs on sand, but we did not sample sandy sites in order to restrict our study to comparable habitat mosaics on relatively steep south-facing slopes. Specifically, we examined the effects of substrate on (1) the pattern of species richness across forest–steppe habitats and the presence of the edge effect, and (2) the beta diversity of forest–steppe landscapes. We then examined the potential effects of these differences on ecosystem-level processes.

2 | METHODS

2.1 | Study sites

The Carpathian Basin is located in southeastern Central Europe. Surrounded by the Alps, the Dinarides, and the Carpathians, it represents an isolated exclave of the forest–steppe biome (Erdős et al., 2018). For this study, we selected 40 sites with preserved forest–steppe mosaics in the western and northern parts of the

Carpathian Basin and in the adjacent hilly areas on its margins, as well as in the Bohemian Karst, which is a relatively dry area in Central Bohemia with forest–steppe vegetation mosaics. The selected sites were in areas with different macroclimates, and the distance between the two most distant sites was 670 km. The sites were on four substrates (Figure 1): (1) andesite, including associated volcanic conglomerates, $n = 7$; (2) dolomite, including dolomitized limestone, $n = 9$; (3) limestone, $n = 14$; and (4) deep soils on loess deposits, including deep loamy soils on calcareous flysch, $n = 10$. Andesite, dolomite and limestone are poorly weathering, hard rocks, whereas loess is a soft sediment. On slopes, hard rocks allow the development of well-drained shallow soil with numerous outcrops, whereas loess gives rise to a deep, loamy soil.

2.2 | Data collection

We selected sites with a preserved mosaic of (near-)natural forest and (near-)natural steppe that were free of relatively recent (not older than 30 years, estimated on site) human interventions such as removal of shrubs or young trees, which is a commonly used conservation measure in steppe grasslands in the study area. At selected sites, which mostly represented a steppe patch embedded in forest, we sampled five 'forest–steppe habitats': (1) forest above the steppe patch ('upper forest'), (2) forest–steppe ecotone above the steppe patch ('upper ecotone'), (3) steppe, (4) ecotone below the steppe patch ('lower ecotone') and (5) forest below the steppe patch ('lower forest'). The steppe patch was mostly located on south-(west-)facing slopes with inclination mainly between 12° and 17°. The upper forest was usually on a slope with the same inclination, but at some sites, especially on dolomite bedrock, the upper ecotone was on the hilltop, and the upper forest was either on a plateau or on usually gentle north-facing slope. The lower forest and lower ecotone were always on slopes with the same aspect as the steppe patch. At each site, we subjectively selected representative spots to sample the five forest–steppe habitats listed above using vegetation plots. The size of each plot was 2.5 m^2 ×4 m^2, with the longer side oriented along the contour line to match the belt shape and orientation of the ecotones. The cover of all vascular plants was recorded using the nine-degree Braun-Blanquet cover-abundance scale (Westhoff & van der

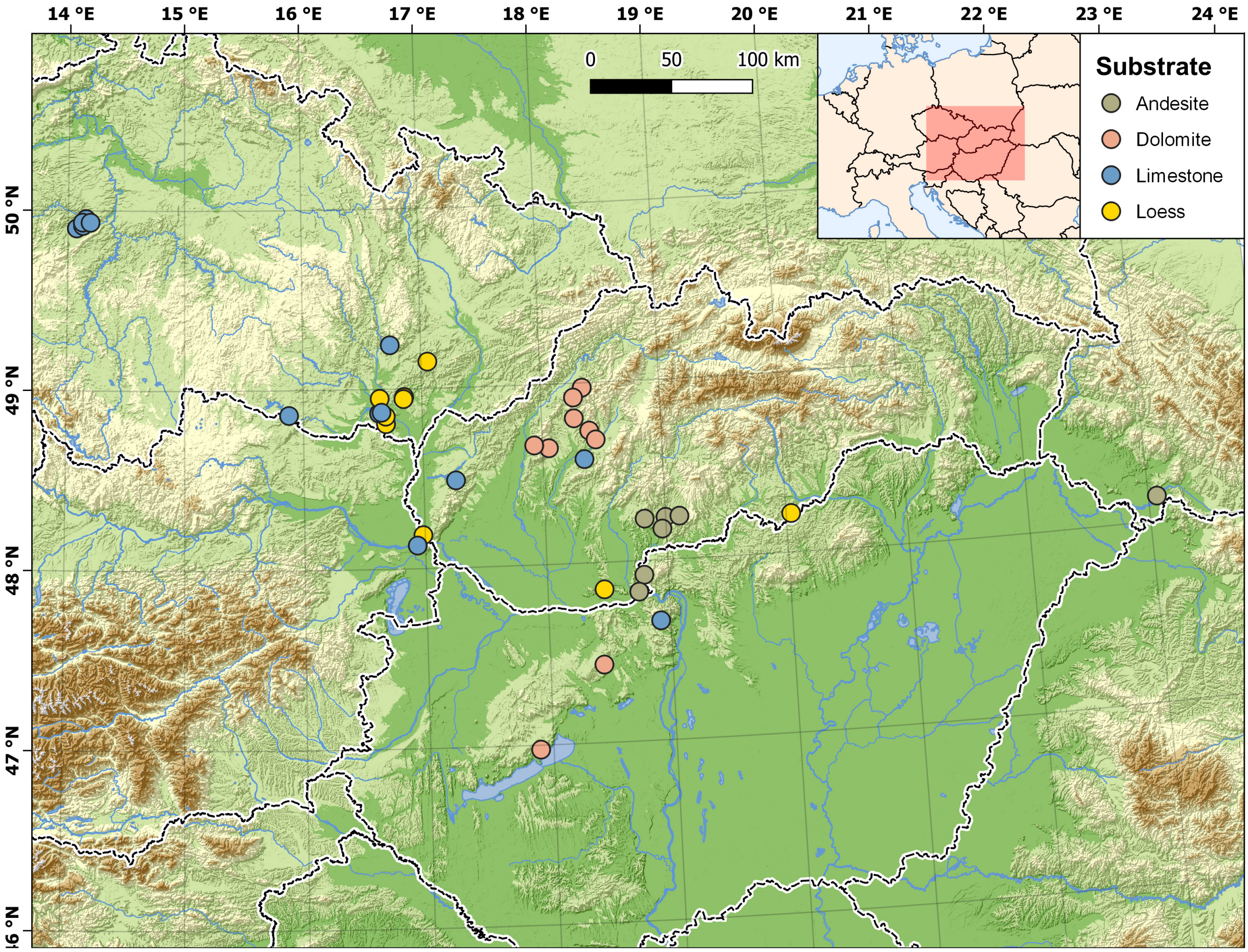

FIGURE 1 Study sites in the northwestern part of the Carpathian Basin and adjacent areas in the Western Carpathians, South Moravia and Central Bohemia (Bohemian Karst)

Maarel, 1978). For each vegetation plot, we estimated the cover of tree, shrub, herb and moss layers, if present. At five sites, the lower forest and lower ecotone were absent or degraded; therefore, we sampled only the other three forest–steppe habitats.

2.3 | Data analysis

To partition variability in species composition of vegetation plots into fractions explained by habitat type, substrate type and site identity, we used distance-based Redundancy Analysis (dbRDA). We also calculated a partial principal coordinate analysis (partial PCoA) to visualise patterns in species composition. In both cases, field-estimated Braun-Blanquet cover values were converted to percentages corresponding to the midpoints of the respective intervals and square-rooted. To calculate the distance matrix, we used the Bray–Curtis dissimilarity measure, which was also square-rooted to avoid negative eigenvalues in the PCoA. In the partial PCoA, we used site identity as a covariate.

To further elucidate the differences in species composition between forest–steppe habitats, we analysed ecological indicator values. Ecological indicator values are species-specific empirically assessed ordinal values on several predefined environmental gradients (such as temperature or moisture), representing the centre of the realized niche of the species on these gradients. Ecological indicator values are usually assessed regionally, and there are several classifications for different regions in Central Europe. We primarily used data for the flora of the Czech Republic (Chytrý et al., 2018) and added data for the Hungarian flora (Borhidi, 1995) for the species that do not occur in the Czech Republic (the selected values with indication of the source can be found in the online repository at https://doi.org/10.5281/zenodo.4783984). We used values for light (scale 1–9 from deep-shade to full-light species), temperature (1–9 from cold-tolerant to heat-demanding species), moisture (1–12 from drought-tolerant to aquatic species), soil reaction (1–9 from acidophilous to basiphilous species) and nutrients (1–9 from species of nutrient-poor sites to those of nutrient-rich sites). We calculated the unweighted community means for all vegetation plots and present the values as boxplots, separately for each substrate type studied.

To assess the distribution of species richness among plots at each site, we calculated deviations from the mean species richness per site for all plots. We plotted the deviations from the per-site mean for each substrate type using boxplots and tested for differences using the Wilcoxon test. We also counted the numbers of shared species between forest–steppe habitats and plotted them in boxplots. For this purpose, we only used the upper forest, upper ecotone and steppe to obtain the same number of vegetation plots at all sites.

Finally, we estimated community biomass based on species height and cover following Axmanová et al. (2012). We used the mean height of mature species from flora manuals (Tutin et al., 1964–1993; Futák et al., 1988 onwards; Kaplan et al., 2019) and multiplied this value by the cover of the respective species in each plot. Finally, we summed these values across all species in the plot to obtain the estimated biomass per plot.

Because we were only interested in the herb layer, we removed trees and shrubs, except for juveniles, from all analyses.

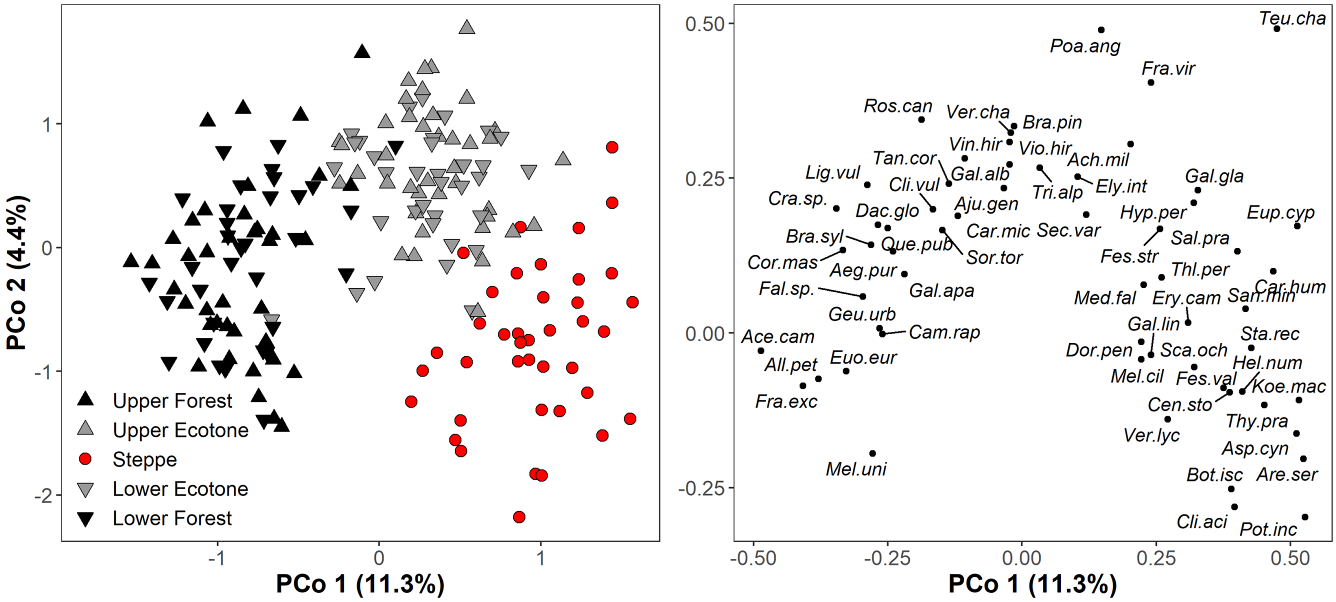

FIGURE 2 Partial principal coordinate analysis (partial PCoA) with site identity as a covariate. As the substrate identity is an aggregation of the site identities, this model also abstracts from the variation caused by the substrate. In the first plot, the colours and symbols represent habitat identity. The second plot shows 30 selected species that occurred in at least three plots and had the highest R^2 and a p-value of 0.01 or less. We used the 'envfit' function for the permutation test to obtain p-values (Oksanen et al., 2019). Species abbreviations refer to the first three letters of the genus name and species epithet (see https://doi.org/10.5281/zenodo.4783984 for full names)

We performed all calculations in R (R Core Team, 2022) using the *tidyverse* package (Wickham, 2017). The ordination model was calculated using the *vegan* package (Oksanen et al., 2019). Nomenclature of vascular plants follows the Euro+Med PlantBase (accessed May 2021) and nomenclature of vegetation types follows EuroVegChecklist (Mucina et al., 2016). Taxa determined only at the genus level were excluded from the data set in all cases in which they potentially contained species already present in the data set (but were not excluded from the species richness counts).

3 | RESULTS

Habitat identity explained 11% ($df = 4$; R^2-adjusted, referring to the constrained variation in dbRDA) of the total variation in species composition, substrate explained 11% ($df = 3$; R^2-adjusted) and site identity explained 26% ($df = 39$; R^2-adjusted). Partial PCoA with site identity as a covariate explained 16% of the total variation by the first two ordination axes (Figure 2). The first axis mainly separated forest from the other two habitats, while the difference between ecotone and steppe was mainly captured by the second axis. There

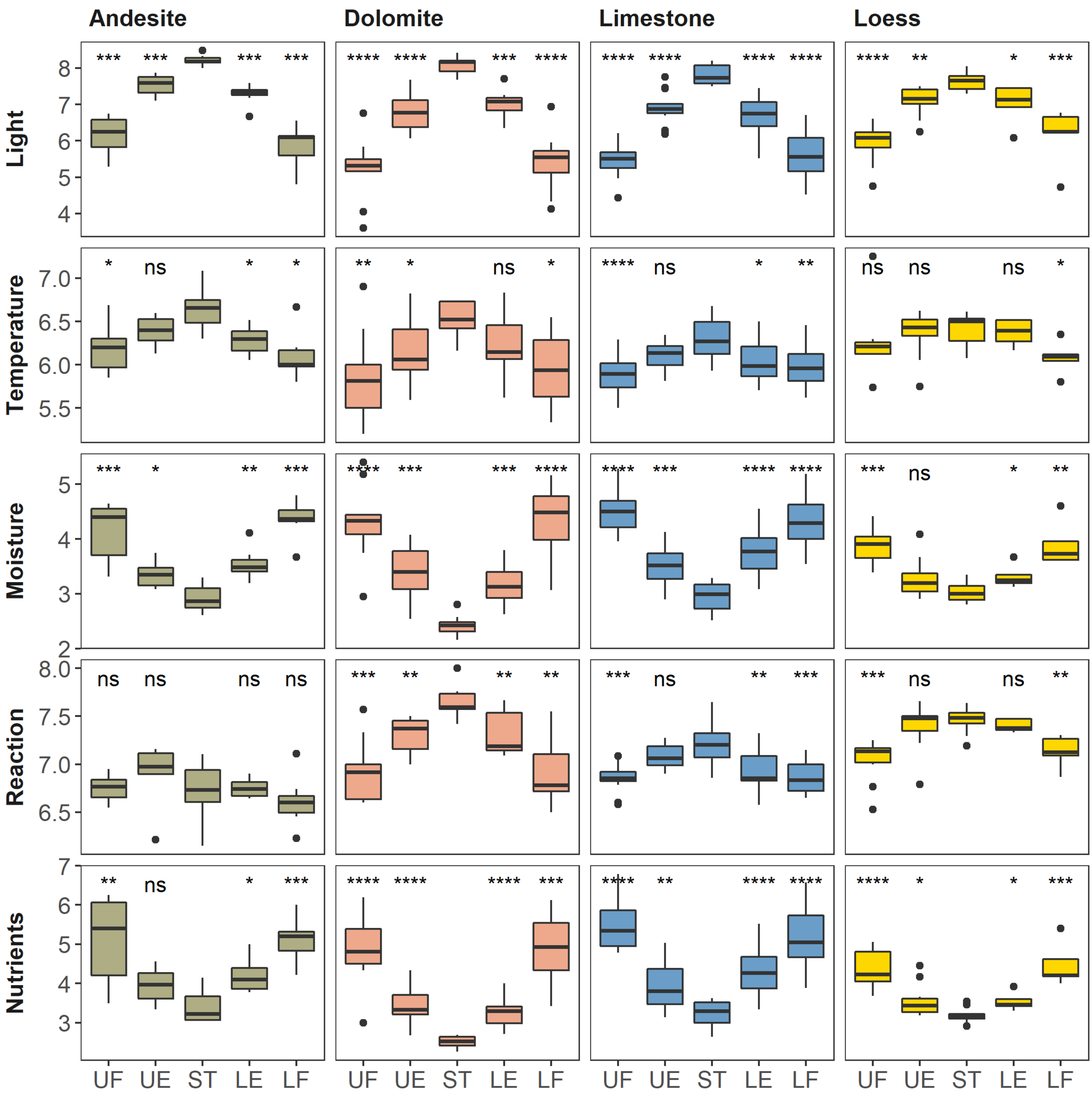

FIGURE 3 Ecological indicator values for five forest–steppe habitats on different substrates. Habitat abbreviations: UF, upper forest; UE, upper ecotone; ST, steppe; LE, lower ecotone; LF, lower forest. Differences from steppe were tested using the Wilcoxon test (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$)

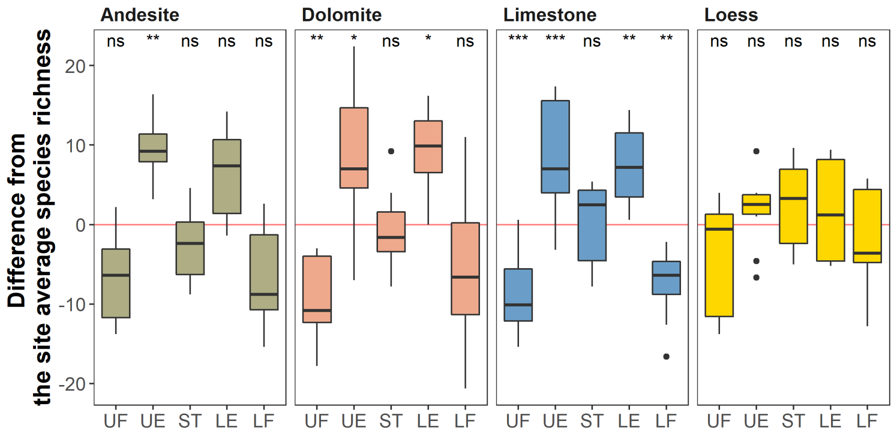

FIGURE 4 The differences in species richness of forest–steppe habitats from the average species richness of individual sites. Habitat abbreviations: UF, upper forest; UE, upper ecotone; ST, steppe; LE, lower ecotone; LF, lower forest. Differences from zero were tested using the Wilcoxon test (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$)

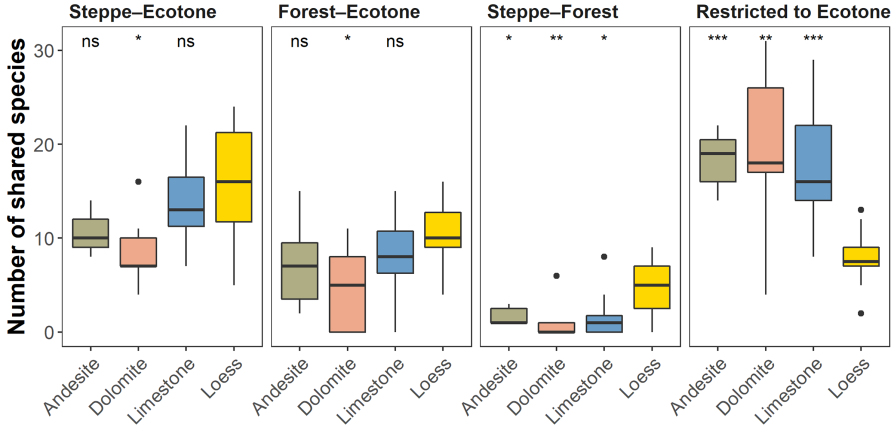

FIGURE 5 The number of species shared by pairs of forest–steppe habitats. For the calculation, we used only the upper forest, upper ecotone and steppe, for which we had all 40 replicates. Differences from loess sites were tested using the Wilcoxon test (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$)

was no noticeable difference in species composition between habitats located above or below the steppe patch. The gradient between forest and steppe was apparent from the distribution of the best-fitting species in the ordination diagram. This analysis indicated that although the ecotone is mostly intermediate plant community between forest and steppe, it also contains some specific species.

The gradual forest–steppe gradient was also reflected in the mean ecological indicator values (Figure 3). Ecotone values were almost always intermediate. However, forest–steppes on hard rock (i.e., andesite, dolomite and limestone) had much wider ranges of indicator values than those on loess. The most pronounced difference was in the distribution of indicator values for moisture and nutrients. The difference between andesite, dolomite and limestone on the one hand and loess on the other hand was also evident in the distribution of species richness among forest–steppe habitats (Figure 4). The former group of substrate types showed a clear pattern of high species richness in ecotone, intermediate richness in steppe and very low richness in forest. In contrast, loess sites had the highest species richness in steppe, intermediate richness in ecotone and lowest richness in forest, although differences among these habitats on loess were not significant.

The intermediate environmental conditions of ecotones were reflected in the high proportion of species shared with adjacent habitats (Figure 5). However, this proportion also differed among substrate types. While it was lowest on dolomite in all comparisons, indicating high beta diversity, it was more than twice as high on loess. The other two substrates fell between these extremes. Among the pairs of forest–steppe habitats, most species were shared between steppe and ecotone. This likely reflects, in part, the overall higher species richness in steppe than in forest, which is most pronounced on dolomite. The number of species found in both forest and steppe was often close to zero, with the exception of loess sites. In contrast, the number of species restricted to ecotones was relatively high on andesite, dolomite and limestone, but low on loess.

Biomass production was generally highest in ecotones (Figure 6). Again, the pattern was determined by the substrate. The increased biomass in ecotones was observed on dolomite and andesite, where all habitats had relatively low productivity. On limestone and loess, ecotone biomass was intermediate between forest and steppe and biomass production was generally higher (Figure 7).

4 | DISCUSSION

At most sites, we observed a positive edge effect, meaning that the ecotones harboured more species than the two adjacent habitats. However, loess sites consistently showed no edge effect, having intermediate species richness in the ecotones. The presence or

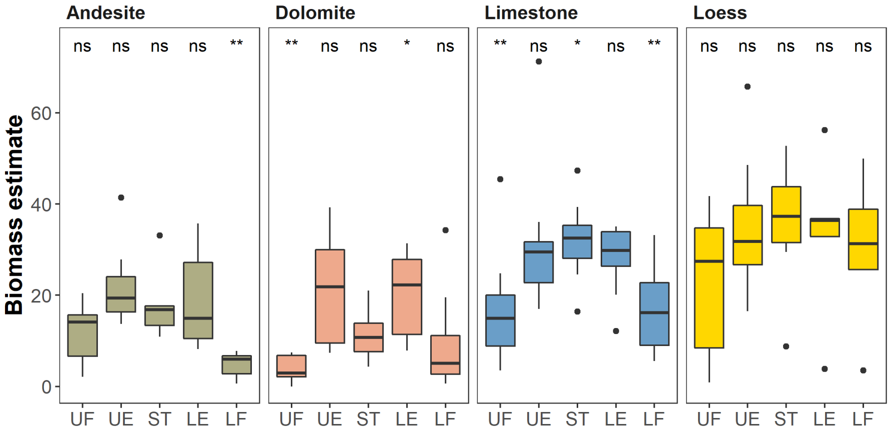

FIGURE 6 Biomass estimates (based on multiplication of species height and cover) for five forest–steppe habitats on different substrates. Habitat abbreviations: UF, upper forest; UE, upper ecotone; ST, steppe; LE, lower ecotone; LF, lower forest. Differences from the substrate-specific overall mean were tested using the Wilcoxon test (***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$)

FIGURE 7 Forest–steppe ecotones on (a) andesite (Súdovce, Štiavnické Mts, Slovakia, 11 June 2020); (b) dolomite (Vinište, Tematínské Hills, Slovakia, 17 June 2020); (c) limestone (Martinka, Pavlov Hills, Czech Republic, 24 May 2020); (d) loess (Milovická stráň, South Moravia, Czech Republic, 22 May 2018). Note the sharp forest edge on andesite, dolomite and limestone and the diffuse forest edge on loess. Photographs by Kryštof Chytrý

absence of an edge effect was not influenced by the location of the ecotone above or below the steppe patch. In terms of species composition, the ecotones hosted a similar number of species occurring also in other forest–steppe habitats, and those that were restricted to them. Monotonic transition from forest to steppe was evident in the distribution of mean indicator values, where ecotones mostly had intermediate values.

4.1 | Edge effects

The positive edge effect and the existence of species restricted to ecotones are important for understanding the nature and maintaining the structure of habitat mosaics in conservation management (Erdős et al., 2014). Therefore, numerous studies have focused on the distribution of species richness, especially in forest–grassland ecotones, with contrasting results and conclusions. For example, the negative edge effect (lower species richness in the ecotone than in adjacent habitats) was observed in scrub–grassland ecotones in agricultural landscapes (Senft, 2009). Others reported the absence of the edge effect, i.e., intermediate species richness in the ecotone compared to adjacent habitats (Lloyd et al., 2000; Erdős et al., 2011; Michalcová, 2016), and probably most studies reported a positive edge effect, including those conducted in semi-natural forest–grassland mosaics (Łuczaj & Sadowska, 1997; Erdős et al., 2019) and natural forest–steppes (Erdős et al., 2014; Tölgyesi et al., 2015). Ecotones depend on their adjacent habitats, which provide a large part of their species pool. The more different the adjacent habitats, the larger the ecotone's species pool could theoretically be. In our study, we found that the manifestation of the edge effect depends on the substrate. On substrates where a positive edge effect occurred, individual forest–steppe habitats were more different from each other. We therefore suggest that the degree of ecotone differentiation depends on the strength of plant community assembly rules, which are largely determined by the nature of the substrate. The strength of assembly rules is likely influenced by a cascade of factors including positive feedback loops (Agnew et al., 1993). However, we do not know what is the primary cause of the differences in community assembly on hard rocks and loess. It may be related to contrasting moisture regimes on shallow soils derived from hard rocks and deep soils derived from loess, which may affect the structure of the tree layer. Nevertheless, these mechanisms need further investigation.

4.2 | Concept of ecotonal vegetation types

The recognition of ecotones as a unique vegetation type has long been the subject of debate among ecologists. As far as phytosociological classification is concerned, the traditional concept proposed by Müller (1962) understands ecotones as a unique vegetation type on the class level (class *Trifolio-Geranietea*). However, this concept was soon criticized (Jakucs, 1970, 1972). This controversy remains up to now. EuroVegChecklist (Mucina et al., 2016) and most national or regional vegetation classifications in Central Europe (e.g. Mucina et al., 1993; Matuszkiewicz, 2007; Willner et al., 2013; Hegedüšová Vantarová & Škodová, 2014) accept Müller's concept of vegetation class for ecotones. However, some authors (e.g., Chytrý, 2007; Borhidi et al., 2012) assigned ecotonal vegetation to the grassland vegetation class *Festuco-Brometea* because of its high floristic similarity with dry grasslands. We found that ecotones indeed share most species with grasslands. However, the number of shared species depends on the substrate: on loess, ecotones generally share more species with adjacent habitats, whereas on poorly weathering hard rocks, the number of species restricted to ecotones is higher, likely due to stronger assembly rules and associated habitat filtering. In addition to differences in species composition, another important aspect considered in vegetation classification is vegetation physiognomy (Mucina, 2019). The phytosociological class *Trifolio-Geranietea* is characterized by high biomass production and the predominance of herbs (Müller, 1962; Mucina et al., 2016; Klinkovská, 2022). For most substrate types, we indeed observed slightly higher biomass production in ecotones than in neighbouring vegetation types, but the difference was small, and in general, biomass production was more comparable to that of steppe than to that of the forest herb layer. Therefore, we suggest that the assignment of ecotonal vegetation in exposure-related forest–steppe mosaics to the separate class *Trifolio-Geranietea* is controversial and requires further investigation.

5 | CONCLUSIONS

In this study, we observed remarkable differences between forest–steppe mosaics formed on hard rocks (i.e., andesite, dolomite and limestone) and loess. The difference between these two types depends partly on the chemistry, but mainly on the physical properties of the soil. While relatively shallow soil develops on hard rocks, the soft parent material supports the development of deep soil on loess. We have shown that the substrate strongly affects numerous properties of forest–steppe mosaics, which may be important for understanding the history of such landscapes, but more urgently for their possible responses to climate change. The strong assembly rules we observed on hard rocks may be more likely to lead to species losses than on soft sediments, where more species find their optimum in more than one forest–steppe habitat.

AUTHOR CONTRIBUTIONS

Kryštof Chytrý designed the study with help of Milan Chytrý, Jan Divíšek and Pavel Novák. Kryštof Chytrý and Helena Prokešová, with contributions of Mário Duchoň, Milan Chytrý, Jan Divíšek and Pavel Novák performed sampling. Kryštof Chytrý performed the analysis and led the writing with contributions of Milan Chytrý, Jan Divíšek and Klára Klinkovská. All authors revised the manuscript.

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DATA AVAILABILITY STATEMENT

The data set containing species composition of vegetation plots and site characteristics is stored in an open-access online repository (https://doi.org/10.5281/zenodo.4783984). The data used for the analyses in this paper are marked there as ‘PART_1’.

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