

RESEARCH ARTICLE

Environmental filtering is the primary driver of community assembly in forest–grassland mosaics: A case study based on CSR strategies

László Erdős^{1,2}  | Khanh Vu Ho^{3,4}  | Ákos Bede-Fazekas^{1,5}  | György Kröel-Dulay¹  | Csaba Tölgyesi⁶  | Zoltán Bátorfi^{6,7}  | Péter Török^{2,8,9} 

¹Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Vácrátót, Hungary

²HUN-REN-UD Functional and Restoration Ecology Research Group, Debrecen, Hungary

³Doctoral School of Environmental Sciences, University of Szeged, Szeged, Hungary

⁴Faculty of Natural Resources-Environment, Kien Giang University, Kien Giang, Vietnam

⁵Department of Environmental and Landscape Geography, Institute of Geography and Earth Sciences, ELTE Eötvös Loránd University, Budapest, Hungary

⁶MTA-SZTE 'Momentum' Applied Ecology Research Group, University of Szeged, Szeged, Hungary

⁷Department of Ecology, University of Szeged, Szeged, Hungary

⁸Department of Ecology, University of Debrecen, Debrecen, Hungary

⁹Polish Academy of Sciences, Botanical Garden – Center for Biological Diversity Conservation in Powsin, Warszawa, Poland

Correspondence

Khanh Vu Ho, Doctoral School of Environmental Sciences, University of Szeged, Szeged, Hungary; Faculty of Natural Resources-Environment, Kien Giang University, Kien Giang, Vietnam. Email: hvkhnh@vnkgu.edu.vn and ho.khanh.vu@stud.u-szeged.hu

Funding information

The National Research, Development and Innovation Office, Hungary (grant number FK 134384 for LE, K 124796 and FK 142428 for ZB, and K 137573 and KKP 144068 for PT); University of Szeged Open Access Fund (Grant number: 6571); The New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund, Hungary (ÚNKP-22-5-SZTE-538 for ZB)

Co-ordinating Editor: Marcos Carlucci

Abstract

Aims: Ecological strategies can provide information about plant community assembly and its main drivers. Our aim was to reveal the dominant strategies of the vegetation types of forest–grassland mosaics and to deduce the assembly processes responsible for their species composition.

Location: Hungary.

Methods: We investigated eight vegetation types of Hungarian forest–steppes. The trade-off between three key traits related to leaf size and economics was used to calculate Grime's competitive–stress tolerance–ruderal (CSR) value for each species, based on which the mean value for each vegetation type was determined. Detrended correspondence analysis (DCA) ordination was used to reveal the compositional differences among the vegetation types under study. To analyze how ecological strategies correlate with the compositional gradient, we used linear regression between plot ordination scores (the first DCA scores) and each strategy (C, S, and R). Linear mixed-effect models were used to evaluate the differences between the vegetation types regarding each strategy (C, S, and R).

Results: Each vegetation type was dominated by the stress-tolerator strategy, indicating the prominent role of environmental filtering in community assembly. However, ecological strategies differed significantly among the communities. The importance of

László Erdős and Khanh Vu Ho contributed equally to this work and are joint first authors.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial-NoDerivs](https://creativecommons.org/licenses/by-nc-nd/4.0/) License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

© 2024 The Authors. *Journal of Vegetation Science* published by John Wiley & Sons Ltd on behalf of International Association for Vegetation Science.

the stress-tolerator strategy decreased toward the less harsh end of the gradient (i.e., from grasslands to forests), while the competitor strategy showed a reverse pattern. The ruderal strategy was weakly correlated with the gradient, although its proportion increased toward the harsh end of the gradient.

Conclusions: With ongoing climate change, an increasing importance of environmental filtering is expected in the assembly of the vegetation types in the studied forest–grassland mosaics. We suggest that CSR strategies offer a useful tool for studying plant-community assembly rules along environmental gradients.

KEYWORDS

competitor, CSR, environmental filter, forest–steppe, leaf trait, ruderal, stress-tolerator

1 | INTRODUCTION

Plant community assembly has long been at the focus of ecological research and remains an issue under intensive scientific discussion (Götzenberger et al., 2012; Dias et al., 2020). Assembly rules determine how species of a regional species pool are selected and fit together to form local communities (Menezes et al., 2020). In addition to its theoretical importance, knowledge of assembly processes has outstanding practical implications as well: it can help to predict plant communities' responses to environmental changes and to restore (near-)natural communities (e.g., Temperton et al., 2004; Münkemüller et al., 2020).

The assembly of plant communities is usually represented as a series of various filters that define which traits (and therefore, which species possessing these traits) can enter the realized local plant community (e.g., Keddy, 1992). The most widespread model includes three filters acting in concert: the dispersal filter determines which species arrive at the site, whereas the environmental filter and the biotic filter select species that can tolerate the local abiotic factors and the biotic interactions from the co-existing species respectively (e.g., Götzenberger et al., 2012; Hulvey & Aigner, 2014; Halassy et al., 2016).

Grime and Pierce (2012) proposed a different scheme, based on three basic ecological phenomena that shape vegetation: competition, stress, and disturbance. According to Grime (1974, 1977) and Grime and Pierce (2012), competition means that co-occurring individuals strive to capture the same units of resource, stress is understood as environmental constraints that limit production, while disturbance is the partial or complete destruction of biomass. Grime and Pierce (2012) argue that every plant species faces an evolutionary trade-off among (1) developing strong competitive ability (competitors, C), (2) withstanding environmental stress (stress tolerators, S), and (3) enduring regular biomass destruction (ruderals, R). According to this view, plants have to pass a filter that favors competitors, stress tolerators, or ruderals in productive, harsh, or disturbed environments respectively. Grime and Pierce (2012) also stressed that there is no hierarchy among the different components of the filter; that is why their model includes a single filter instead of a series of filters.

As emphasized by Grime and Pierce (2012), there are no living beings that would be exclusively C-, S-, or R-selected. For example, a species that shows a high degree of C-selection also has to cope with some level of S- and R-selection. This means that in reality, individuals have to pass all three components of the CSR-filter, even though each component may represent a greater or smaller obstacle.

The filter proposed by Grime and Pierce (2012) selects individuals possessing traits that are directly beneficial to competitive ability, stress tolerance, and the survival of the population by completing the individual life cycle between two destructive events. These traits (i.e., traits that are directly connected to the CSR strategies) display a plant's general strategy. Consequently, by studying the traits and strategies of the species composing a plant community, we can gather information about the primary drivers that determine community composition.

In the forest–steppe zone, which is a transitional zone between closed-canopy forests and steppes (Erdős et al., 2018a), it is assumed that forest and grassland patches, in most cases, represent alternative stable states, that is, they appear under the very same primary environmental conditions and are stable in time (Petraitis, 2013; Erdős et al., 2023). However, secondary differences emerge among the patches, evoked by the vegetation itself, further stabilizing the pattern of the individual patches. For example, trees and shrubs increase the humus and moisture content of the upper soil and mitigate daily temperature extremes, changes that favor the continuous existence of the forest and hinder the establishment of grassland species (Erdős et al., 2023). As a result, significant environmental differences have been revealed among the various plant communities, which can be arranged along an environmental harshness gradient (Erdős et al., 2018b, 2020; Ho et al., 2024). Generally, daytime temperatures in the growing season are low in large forest patches and increase through smaller-sized forest patches and edges to grasslands, which are the hottest habitats, especially in summer. Nighttime temperatures show a reverse trend, and thus, large forests have the lowest and grasslands the highest daily temperature fluctuations. Both the moisture content of the upper soil layer and daytime air humidity

are the highest in large forest patches and become progressively lower toward smaller-sized forest patches and edges, and are the lowest in grasslands.

In this study, our aim was to reveal the dominant strategies of the vegetation types of sandy forest–steppes, and infer the assembly processes responsible for their species composition. We hypothesized that in the more productive environment of forest patches, community composition would be driven by competitive exclusion, while under the harsher conditions of open grasslands, stress (i.e., environmental filtering) would be the most important driver—expressed also in the composition of traits.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in the Kiskunság Sand Ridge in central Hungary, a lowland area in the heart of the Carpathian Basin between the rivers Danube and Tisza. We selected thirteen legally protected sites with near-natural vegetation (Figure 1a; Appendix S1). The subcontinental climate with sub-Mediterranean influences is characteristic of this region with an average annual temperature of

10.3–10.5°C and an average annual precipitation of 520–550 mm (Tölgyesi et al., 2016). Grasslands have humus-poor sandy soil with low water retention capacity (Várallyay, 1993); however, the humus content is slightly higher in forest patches (Erdős et al., 2014).

The area belongs to the westernmost outposts of the forest–steppe zone. Although the overwhelming majority of forest–steppe ecosystems of the region have been converted to agricultural fields or tree plantations (Molnár et al., 2012), a few sandy forest–steppe areas have survived and are currently under legal protection. Within the study sites, the vegetation is characterized by a mosaic-like pattern of forest and grassland patches (Figure 1b). The variously sized forest patches of poplar–juniper stands (*Junipero-Populetum albae*) exhibit a cover of 50%–80% and are dominated by *Populus alba* with heights ranging from 10 m to 15 m. In the shrub layer, typical species include *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, *Ligustrum vulgare*, and *Prunus spinosa*, and their cover ranges from 5% to 80%. The herb layer hosts species such as *Carex liparocarpus*, *Cynoglossum officinale*, *Euphorbia cyparissias*, and *Teucrium chamaedrys*. Forest patches range in size from a few dozen square meters to as large as 1 ha.

There are three types of grasslands in the study sites. The closed perennial grassland (*Astragalo austriacae-Festucetum rupicola*), which has a relatively high cover (typically more than 80%),

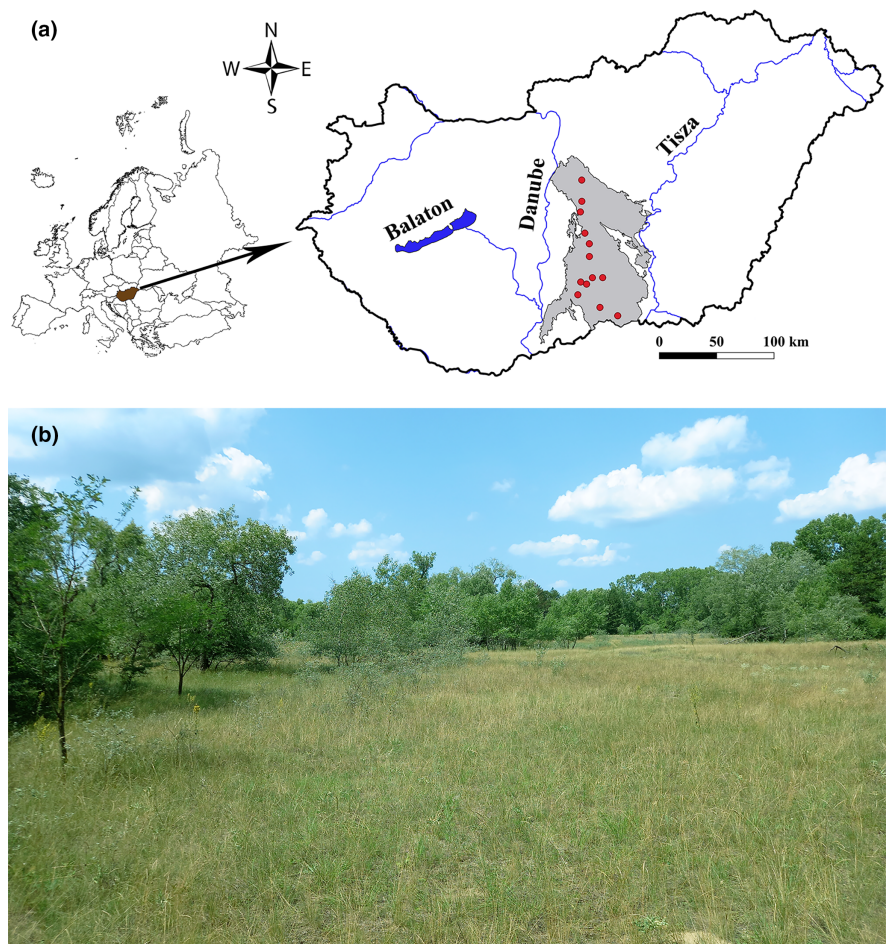


FIGURE 1 (a) The location of Hungary in Europe (brown) and thirteen study sites (red dots) in the Kiskunság Sand Ridge (gray) in central Hungary. (b) A mosaic of forests and grasslands in the study region.

is dominated by *Festuca rupicola*, *Stipa borysthenaica*, and *Stipa capillata*. Other typical species are, among others, *Achillea pannonica*, *Calamagrostis epigejos*, *Euphorbia cyparissias*, and *Poa angustifolia*.

The most widespread grassland type is the open perennial grassland (*Festucetum vaginatae*), which is dominated by *Festuca vaginata*, *Stipa borysthenaica*, and *Stipa capillata*. The overall total vascular vegetation cover varies between 40% and 70%. Other typical species include *Alkanna tinctoria*, *Centaurea arenaria*, *Koeleria glauca*, and *Syrenia cana*.

The open annual grassland vegetation (*Secali sylvestris-Brometum tectorum*) has a vascular vegetation cover of 20%–50% and is dominated by *Bromus tectorum* and *Secale sylvestre*. Other common species include *Bromus squarrosus*, *Poa bulbosa*, *Silene conica*, and *Viola arvensis*.

Plant species nomenclature is in accordance with Király (2009), while plant association names are based on Borhidi et al. (2012).

2.2 | Field sampling

We distinguished and analyzed eight vegetation types at each site: large forest patches (>0.5 ha), medium forest patches (0.2–0.4 ha), small forest patches (<0.1 ha), north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands. Based on the earlier studies of Erdős et al. (2018b, 2020), we used 5 m × 5 m plots for sampling forest interiors and grasslands, while 2 m × 12.5 m plots were employed to study forest edges, preventing their extension into the interiors of the adjacent vegetation types. In this study, we defined an edge as the area outside of the outermost tree trunks but still under the canopy. Edge plots were established along the relatively straight peripheral zones of forest patches that were larger than 0.2 hectares in size.

A total of 494 plots were used: 60 plots in large forest patches, 64 plots in medium forest patches, 60 plots in open annual grasslands, 50 plots in closed perennial grasslands, and an equal count of 65 plots in each of the other vegetation types (Appendix S1). The number of replicates was determined by the lack or rarity of certain vegetation types at some study sites. We visually estimated the cover of all vascular plant species in all vegetation layers (canopy, shrub, and herb) in each plot in spring (April–May) and summer (July–August). The highest cover value for each species was then applied for subsequent data analyses. Seven taxa unidentified at the species level (*Acer* sp., *Epipactis* sp., *Fraxinus* sp., *Hieracium* sp., *Lathyrus* sp., *Prunus* sp., and *Silene* sp., none of which was found in more than three of the 494 plots), were excluded from the analyses involving strategy.

2.3 | Leaf traits and ecological strategies

To determine the strategy of the species, three leaf traits were used: leaf area (LA, mm²), leaf dry matter content (LDMC, mg/g),

and specific leaf area (SLA, mm²/mg), based on the observation that species with the C strategy invest resources in increasing LA; species with the S strategy invest in retaining LDMC; and species with the R strategy invest primarily in the ability to increase SLA (Pierce et al., 2017). It is widely accepted that these traits strongly represent the leaf economics and plant size spectra (sensu the global spectrum of plant form and function; Díaz et al., 2016). Trait data were extracted from Hungarian databases (Lhotsky et al., 2016a, 2016b; E-Vojtkó et al., 2020; Gyalus et al., 2022; McIntosh-Buday et al., 2022). Data were retrieved from PADAPT, the Pannonian Database of Plant Traits (Sonkoly et al., 2023). However, eight of the 289 taxa (2.77%) did not have SLA data in this database. Therefore, we used the LEDA database published by Kleyer et al. (2008) to provide missing values for these species.

We calculated the strategy (separate C, S, and R values) for each species based on the trade-off among the three above leaf traits by the “StrateFy” tool, which regresses trait values against the principal component analysis (PCA) axes extracted from global leaf traits (Pierce et al., 2017). This method enables determining CSR values for a wide range of vascular plant species globally (Pierce et al., 2017). Based on the C, S, and R components of the strategy for each species, we calculated both the unweighted and weighted mean C, S, and R values for each plot, using presence/absence data for the former situation and square-root-transformed cover scores for the latter one.

2.4 | Data analysis

To analyze the differences in species composition among the vegetation types, we applied detrended correspondence analysis (DCA), which was performed on square-root-transformed cover scores. Detrending was performed using the default number of rescaling cycles (4) and segments (26). The first DCA axis was used for the quantification of vegetation types along the compositional gradient, which provides a continuous number interpretable as “compositional similarity to open grassland” or “compositional dissimilarity to a large forest.” The analysis was conducted using the *vegan* package in R version 4.1.2 (R Core Team, 2021; Oksanen et al., 2022).

For all vegetation types, the strategy values (C, S and R) per plot were visualized using a ternary graph, which was created using the *ggtern* package in R (Hamilton & Ferry, 2018).

To reveal how ecological strategies (C, S, and R) correlate with the gradient, we used linear regression between plot ordination scores (the first DCA scores) and each strategy (C, S, and R). The models were visually checked using the diagnostic plots.

To evaluate the differences between the vegetation types regarding each strategy (C, S, and R), we used linear mixed-effect models. In our modeling approach, the site was treated as a random factor, while the vegetation type was considered a fixed factor. We applied the *glmmTMB* package in R to construct the models, using the Gaussian family distribution (Brooks et al., 2017). The models were visually checked using the *performance* package in

R (Lüdecke et al., 2021). In order to find a significant proportion of variability, an analysis of variance was performed on the linear mixed-effect models. Afterwards, we used the *emmeans* package to perform pairwise comparisons among the levels of the fixed factor and adjusted the *p*-values using the Bonferroni method (Lenth, 2022).

3 | RESULTS

The DCA ordination revealed a compositional gradient along the first DCA axis with the following order of vegetation types: large forest patches—medium forest patches—small forest patches—north-facing edges—south-facing edges—closed perennial grasslands—open perennial grasslands—open annual grasslands (Figure 2). It demonstrated that the first DCA scores can be used in the subsequent analyses and interpreted as a compositional gradient.

The ternary plot showing unweighted values revealed that the average CSR values were located along the RS-axis with a smaller contribution from component C (Figure 3a). The contributions of mean components S and R were 50%–60% and 20%–30% respectively. The study found a smaller contribution from mean component C (<25%). When taking a closer look (Figure 3b), a separation between values across vegetation types was found, forming different groups: large and medium forest patches belonged to one group, small forest patches, north- and south-facing edges, and closed grasslands formed another group, and open perennial and open annual grasslands formed the third group. Generally, the ternary plot based on weighted values showed a rather similar pattern (Appendix S2).

The scores of the sample plots on the primary ordination axis were negatively associated with the C strategy (Figure 4a) but positively associated with the S strategy (Figure 4b). A weak but positive relation was observed between the R strategy and DCA1 scores (Figure 4c). The vegetation type affected each type of strategy as

follows: component C ($\chi^2 = 1637$, $p < 0.001$), component S ($\chi^2 = 242$, $p < 0.001$), and component R ($\chi^2 = 123$, $p < 0.001$). Based on the pairwise comparisons (Appendix S3), the highest component C was found in large and medium forest patches, and it gradually decreased toward the end of the vegetation gradient (Figure 4d). Component S depicted a gradually increasing trend from large forest patches to open annual grasslands (Figure 4e). Open perennial and annual grasslands exhibited the highest component R, whereas north-facing edges displayed the lowest component R (Figure 4f). Again, patterns were similar with weighted values, although some differences did emerge (Appendix S4). For example, component S had a more equal presence along the gradient for weighted than for unweighted values, and the relationship was more hump-backed. In addition, there was a more pronounced change of component R along the gradient for weighted than for unweighted values.

4 | DISCUSSION

In this work, we studied the vegetation types of forest–grassland mosaics in eastern Central Europe. In the framework of the CSR theory (Grime & Pierce, 2012), it is possible to infer community assembly processes from the strategies of plant communities. For example, if a plant community is dominated by the competitor strategy, this suggests that the competition filter is the most notable obstacle for individuals to enter the realized local plant community. However, as already noted in the Introduction, no species can be regarded as exclusively C-, S-, or R-selected, which also applies to communities. Thus, a given plant community that is dominated by the competitor strategy also has a certain level of environmental stress and disturbance. Moreover, there may be additional drivers shaping plant communities, such as dispersal, which is not assessed by the CSR approach used in the present work.

The eight studied vegetation types formed a compositional gradient (Figure 2). Generally, each vegetation type was dominated

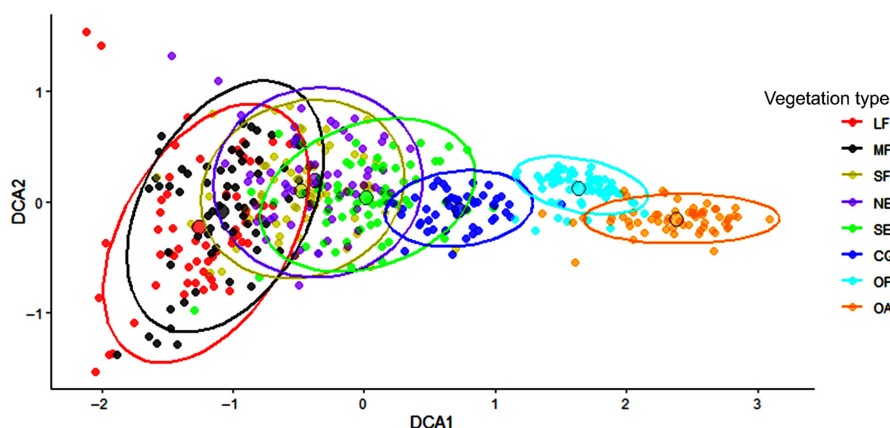


FIGURE 2 DCA ordination scattergram of the 494 plots. Large symbols indicate the centroids for each vegetation type. Ordination ellipses were drawn based on standard deviation of point scores, where the directions of the major axes of the ellipses were defined by the weighted correlation. CG, closed perennial grasslands; LF, large forest patches; MF, medium forest patches; NE, north-facing forest edges; OA, open annual grasslands; OP, open perennial grasslands; SE, south-facing forest edges; SF, small forest patches.

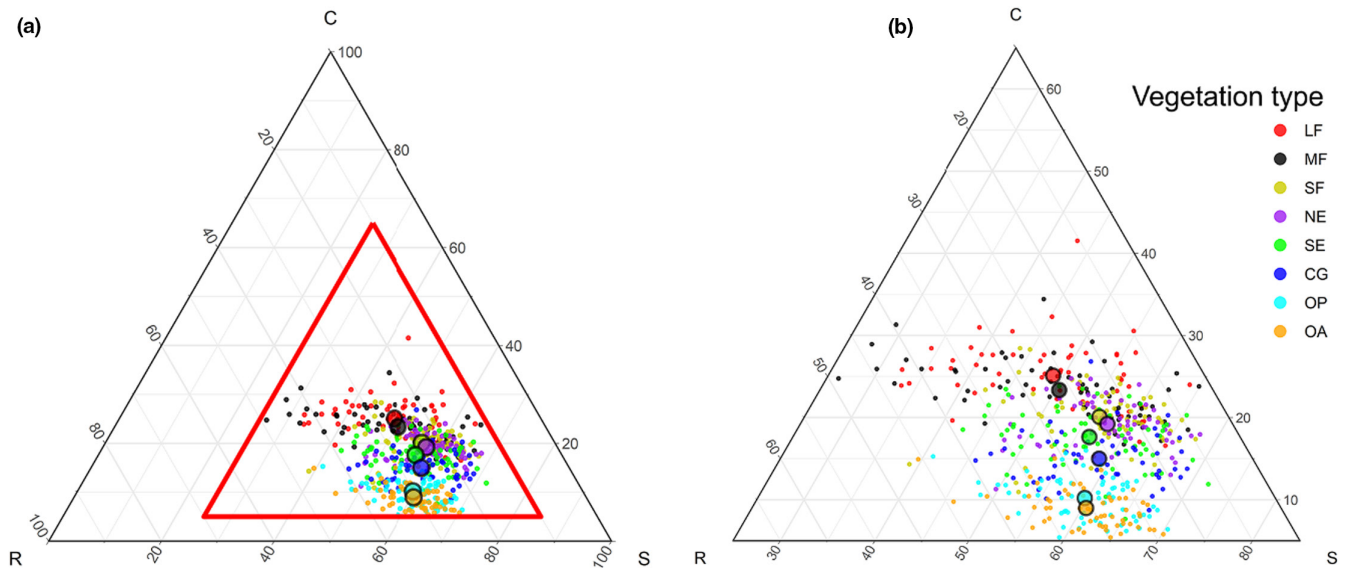


FIGURE 3 Ternary plots showing unweighted mean values of CSR strategies for the eight vegetation types. The red triangle in plot (a) shows the boundaries of plot (b). Larger symbols indicate the mean value for each vegetation type. Vegetation type abbreviations are according to the caption of Figure 2.

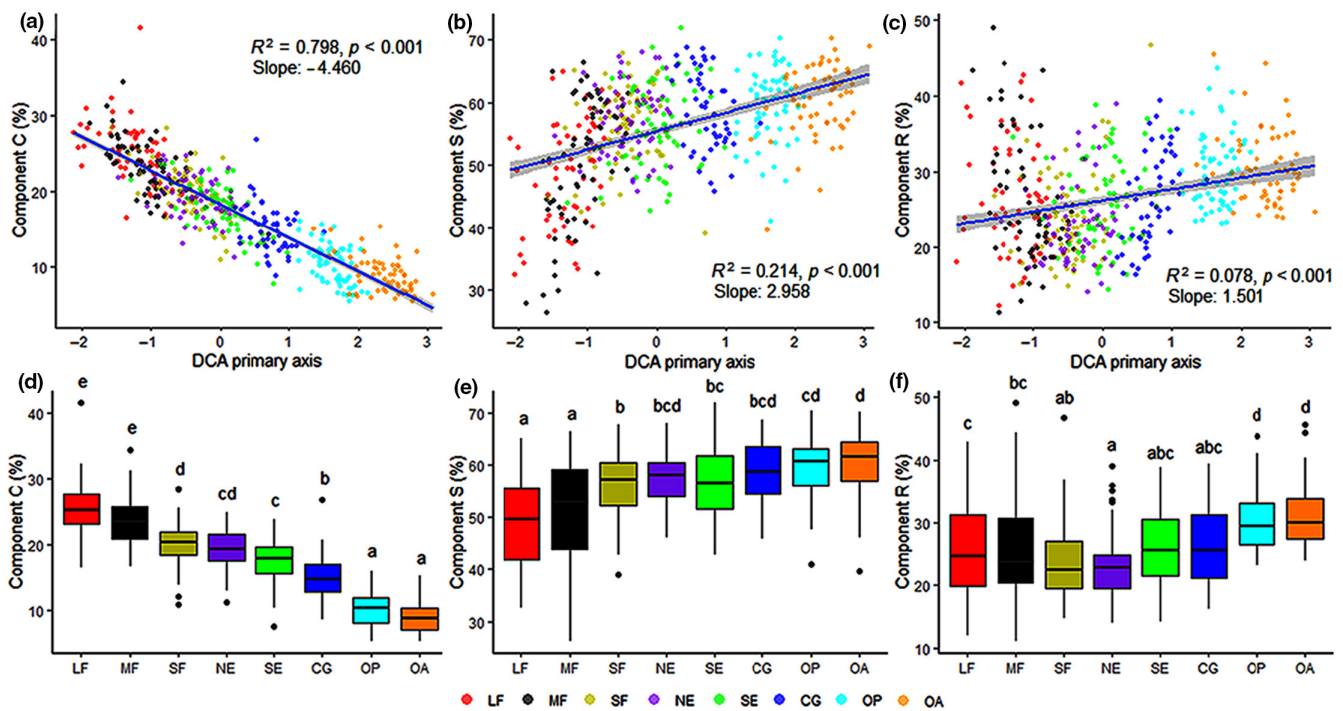


FIGURE 4 Relationships between plot scores on the primary DCA ordination axis and each unweighted strategy component: (a) C; (b) S, and (c) R; p -value and adjusted R -squared were calculated using linear regression; Slope: the slope value of the regression line; the blue line is the regression line, and the gray area around the line represents the 95% confidence interval. Box plots demonstrate the variability of each strategy component: (d) C, (e) S, and (f) R in the eight communities. Those that do not share a letter are significantly different at the significance level of $\alpha = 0.05$. Vegetation type abbreviations are according to the caption of Figure 2.

by the stress-tolerator strategy (Figure 3a), which reflects the relatively harsh environmental conditions prevailing in the study region. According to Grime and Pierce (2012), stress-tolerator plant species have an advantage over other species in unproductive and variable environments. In the Kiskunság Sand Ridge, most species encounter a harsh environment, as the amount of precipitation is low and shows

high interannual variations (from <350 mm in some years to >800 mm in others) (Tölgyesi et al., 2016). The very low water retention capacity of the sandy soils in the region, alongside their low humus content (Várallyay, 1993) further increase the environmental stress.

Although each vegetation type examined in the present work was dominated by the stress-tolerator strategy, ecological



strategies differed markedly among the studied vegetation types (Figures 3b and 4). This is similar to the findings of Rosenfield et al. (2019), who revealed distinct plant strategies along a relatively short gradient in South America. In our study region, competition proved to be a relatively important force in community assembly in large and medium forest patches, while its importance progressively diminished along the gradient toward the grasslands. Competition seemed to play the most subordinate role in the open grassland vegetation. The stress-tolerator strategy showed a reverse trend. Our environmental measurements (Erdős et al., 2018b; Ho et al., 2024) suggest that the forests of the study region are more productive and less harsh than grasslands, with forest edges typically providing intermediate environments. Trees and shrubs reduce environmental stress by providing relatively cool and humid circumstances under the canopy during the growing season, including the hot and dry months of late summer. Also, the canopy reduces daily temperature variation and mitigates extremes. In addition, forests have increased soil moisture and improved soil humus content compared to grasslands. Thus, our results are consistent with the predictions of Grime and Pierce (2012) and Adler et al. (2013), who argued that along productivity gradients, a shift in the importance of abiotic vs biotic factors can be expected, with abiotic constraints becoming more important toward the harsh end (in our case, grasslands) and competition becoming more important toward the more productive end of the gradient (in our case, forests). Our results also fit the findings of Dayrell et al. (2018), who reported that in south-east Brazil competition dominates community assembly in forest patches, whereas environmental stress is more important in grasslands. Similarly, Negreiros et al. (2014) claim that grasslands, especially those in highly unproductive environments, tend to be dominated by the stress-tolerator strategy.

When using weighted instead of unweighted values (Appendix S4), the importance of stress was further emphasized, as component S was high throughout the full gradient, and differences among the habitats were only moderate. Since filters have an influence on species' abundances in a given community, this reinforces our findings with unweighted values and makes our results more robust. The somewhat hump-backed shape of the curve suggests that stress loses some importance toward the end points of the gradient, probably because competition becomes more important in large and medium forest patches, while disturbance increases in importance in the open annual grasslands.

We suggest that competition for light is an important force that shapes forest communities in the study region, while competition for water and nutrients may be more limited in this vegetation type. The herb layer is sparse and individuals are usually widely spaced, suggesting low levels of competition, especially because the upper soil layer is relatively moist (Erdős et al., 2018b). Woody species reach much deeper soil layers, resulting in reduced competition between them and herbs.

We found obvious differences in strategies among the differently sized forest patches and the forest edges, suggesting that

smaller forest patches and forest edges have a limited ability to buffer environmental stress (Erdős et al., 2023), that is, they are harsher than the larger forest patches.

Focusing on the three grassland types, competition seems to be more important and stress tolerance slightly less important in closed grasslands than in open ones. Similarly, comparing different grasslands of the Tibetan Plateau, Yu et al. (2022) showed that the importance of competition increased and the importance of stress tolerance decreased with increasing productivity. Kelemen et al. (2013) compared various lowland grassland communities and found that competition was more important in stable and productive environments, whereas stress-tolerator species gained advantage in alkaline and highly variable environments. The fact that stress tolerance is more important in open grasslands than in closed ones may reflect the harsher conditions in the former types (Ho et al., 2024). In closed grasslands, there is probably intensive competition both for light (above ground) and water and nutrients (below ground). In contrast, the widely spaced individuals in open grasslands probably experience less competition. Open annual grasslands, in particular, contain individual plants scattered on a relatively open surface, with small roots and limited leaf surfaces, suggesting weak competition.

When using unweighted values, the R strategy was only weakly related to DCA1 scores (Figure 4c) and played the most important role in the open grassland types (Figure 4f). With weighted values, however, the R strategy was much more strongly related to DCA1 scores, and this strategy proved much more important in open annual grasslands than in open perennial grasslands (Appendix S4). The R strategy is typical in early successional stages, on open, recently exposed surfaces (e.g., Caccianiga et al., 2006), which fits our findings. The open perennial grassland (OP) has considerable open sand surfaces between the dominant tussock grasses, where small annual plants are typical, similarly to other vegetation types with an important contribution of component R (Li & Shipley, 2017; Pierce et al., 2017). Open annual grasslands (OA) usually emerge as a result of disturbance, most often wind erosion or trampling by grazers and browsers (Fekete, 1992; Borhidi et al., 2012), although identifying the exact disturbance agents needs further research.

To sum up, our hypothesis that community assembly would be dominated by competitive exclusion in the forest patches and stress (i.e., environmental filtering) would dominate in grasslands was supported only partly. While it is true that the importance of competition was larger in woody habitats (i.e., forests and edges) than in grasslands, environmental filtering was the most important factor in each of the vegetation types (Figure 5). Disturbance played the most important role in the open perennial and the open annual grassland communities.

A significant drying tendency has been observed in Hungary during the last few decades (Jaagus et al., 2022), and the trend is projected to continue during the 21st century (Sábitz et al., 2014). As a result, we expect that vegetation types become even more stressed by aridity. This may result in increasing importance of environmental filtering, which already dominates the assembly of the plant communities in the Kiskunság Sand Ridge.

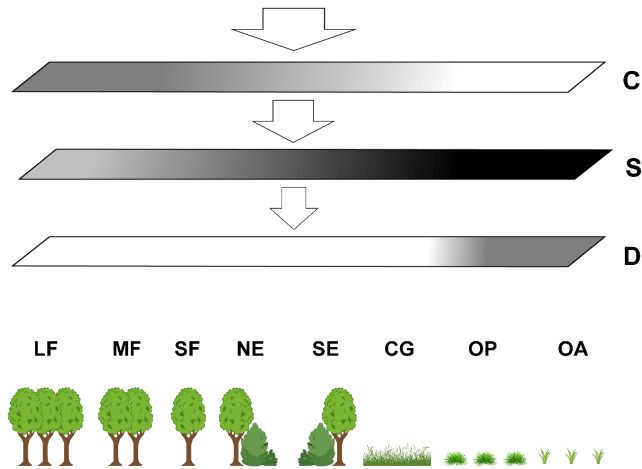


FIGURE 5 Assembly in the eight studied vegetation types of the forest–grassland mosaics in the Kiskunság Sand Ridge. The three components of the filter proposed by Grime and Pierce (2012) are shown as separate filters to increase clarity, but their order should not be interpreted as a hierarchy. Darker colors indicate dominating role of a filter. C, competition; D, disturbance; S, stress. Vegetation type abbreviations are according to the caption of Figure 2.

Similar to Catorci et al. (2011) and Han et al. (2021), we found that the CSR strategy types offer a useful tool for the study of plant-community assembly rules along gradients. However, a considerable limitation of our study was the limited length of the gradient. Studies encompassing more productive (and at the same time, less harsh) vegetation types (such as Lhotsky et al., 2016a, 2016b), or studies that contain a longer section of the disturbance gradient (e.g., Pierce et al., 2007) could provide additional information on assembly rules.

AUTHOR CONTRIBUTIONS

László Erdős designed the study, László Erdős, Khanh Vu Ho, Ákos Bede-Fazekas, György Kröel-Dulay, Csaba Tölgyesi, Zoltán Bátor, and Péter Török conducted the field works, Khanh Vu Ho and Ákos Bede-Fazekas analyzed the data, László Erdős, Khanh Vu Ho, Ákos Bede-Fazekas, György Kröel-Dulay, Csaba Tölgyesi, Zoltán Bátor, and Péter Török interpreted the results, László Erdős and Khanh Vu Ho wrote the first draft of this manuscript, and László Erdős, Khanh Vu Ho, Ákos Bede-Fazekas, György Kröel-Dulay, Csaba Tölgyesi, Zoltán Bátor, and Péter Török edited the manuscript.

ACKNOWLEDGEMENTS

The authors thank Dolly Tolnay for her help with the trait databases. We would also like to acknowledge the financial support from the János Bolyai Research Scholarship of the Hungarian Academy of Sciences to Zoltán Bátor and László Erdős, and the Stipendium Hungaricum Scholarship for Khanh Vu Ho.

FUNDING INFORMATION

The National Research, Development and Innovation Office, Hungary (grant number FK 134384 to László Erdős; K 124796 and FK 142428 to Zoltán Bátor; and K 137573 and KKP 144068 to Péter

Török). The New National Excellence Program of the Ministry for Culture and Innovation from the source of the National Research, Development and Innovation Fund, Hungary (ÚNKP-22-5-SZTE-538 to Zoltán Bátor). University of Szeged Open Access Fund (Grant number: 6571).

DATA AVAILABILITY STATEMENT

Data necessary to reproduce the analyses are deposited at Zenodo: <https://doi.org/10.5281/zenodo.10255319> (Erdős et al., 2023).

ORCID

László Erdős <https://orcid.org/0000-0002-6750-0961>
 Khanh Vu Ho <https://orcid.org/0000-0002-9117-7789>
 Ákos Bede-Fazekas <https://orcid.org/0000-0002-2905-338X>
 György Kröel-Dulay <https://orcid.org/0000-0002-0695-1232>
 Csaba Tölgyesi <https://orcid.org/0000-0002-0770-2107>
 Zoltán Bátor <https://orcid.org/0000-0001-9915-5309>
 Péter Török <https://orcid.org/0000-0002-4428-3327>

REFERENCES

- Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. (2013) Trait-based tests of coexistence mechanisms. *Ecology Letters*, 16, 1294–1306. Available from: <https://doi.org/10.1111/ele.12157>
- Borhidi, A., Kevey, B. & Lendvai, G. (2012) *Plant communities of Hungary*. Budapest: Academic Press.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400. Available from: <https://doi.org/10.3929/ethz-b-000240890>
- Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M. & Cerabolini, B. (2006) The functional basis of a primary succession resolved by CSR classification. *Oikos*, 112, 10–20. Available from: <https://doi.org/10.1111/j.0030-1299.2006.14107.x>
- Catorci, A., Vitanzi, A. & Tardella, F.M. (2011) Variations in CSR strategies along stress gradients in the herb layer of submediterranean forests (Central Italy). *Plant Ecology and Evolution*, 144, 299–306. Available from: <https://doi.org/10.5091/plevevo.2011.621>
- Dayrell, R.L.C., Arruda, A.J., Pierce, S., Negreiros, D., Meyer, P.B., Lambers, H. et al. (2018) Ontogenetic shifts in plant ecological strategies. *Functional Ecology*, 32, 2730–2741. Available from: <https://doi.org/10.1111/1365-2435.13221>
- Dias, A.T.C., Rosado, B.H., De Bello, F., Pistón, N. & De Mattos, E.A. (2020) Alternative plant designs: consequences for community assembly and ecosystem functioning. *Annals of Botany*, 125, 391–398. Available from: <https://doi.org/10.1093/aob/mcz180>
- Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S. et al. (2016) The global spectrum of plant form and function. *Nature*, 529, 167–171. Available from: <https://doi.org/10.1038/nature16489>
- Erdős, L., Ambarli, D., Anenkhonov, O.A., Bátor, Z., Cserhalmi, D., Kiss, M. et al. (2018a) The edge of two worlds: a new review and synthesis on Eurasian forest-steppes. *Applied Vegetation Science*, 21, 345–362. Available from: <https://doi.org/10.1111/avsc.12382>
- Erdős, L., Ho, K.V., Bátor, Z., Kröel-Dulay, G., Ónodi, G., Tölgyesi, C. et al. (2023) Taxonomic, functional, and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics. *Journal of Ecology*, 111, 182–197. Available from: <https://doi.org/10.1111/1365-2745.14025>
- Erdős, L., Kröel-Dulay, G., Bátor, Z., Kovács, B., Németh, C., Kiss, P.J. et al. (2018b) Habitat heterogeneity as a key to high conservation

- value in forest-grassland mosaics. *Biological Conservation*, 226, 72–80. Available from: <https://doi.org/10.1016/j.biocon.2018.07.029>
- Erdős, L., Tölgyesi, C., Horzse, M., Tolnay, D., Hurton, A., Schulcz, N. et al. (2014) Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. *Ecological Complexity*, 17, 107–118. Available from: <https://doi.org/10.1016/j.ecocom.2013.11.004>
- Erdős, L., Török, P., Szitár, K., Bátori, Z., Tölgyesi, C., Kiss, P.J. et al. (2020) Beyond the forest-grassland dichotomy: the gradient-like organization of habitats in forest-steppes. *Frontiers in Plant Science*, 11, 236. Available from: <https://doi.org/10.3389/fpls.2020.00236>
- E-Vojtkó, A., Balogh, N., Deák, B., Kelemen, A., Kis, S., Kiss, R. et al. (2020) Leaf trait records of vascular plant species in the Pannonian flora with special focus on endemics and rarities. *Folia Geobotanica*, 55, 73–79. Available from: <https://doi.org/10.1007/s12224-020-09363-7>
- Fekete, G. (1992) The holistic view of succession reconsidered. *Coenoses*, 7, 21–29.
- Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A. et al. (2012) Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological Reviews*, 87, 111–127. Available from: <https://doi.org/10.1111/j.1469-185X.2011.00187.x>
- Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, 250, 26–31. Available from: <https://doi.org/10.1038/250026a0>
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111, 1169–1194.
- Grime, J.P. & Pierce, S. (2012) *The evolutionary strategies that shape ecosystems*. Chichester: John Wiley & Sons.
- Gyalus, A., Barabás, S., Berki, B., Botta-Dukát, Z., Kabai, M., Lhotsky, B. et al. (2022) Plant trait records of the Hungarian and Serbian flora and methodological description of some hardly measurable plant species. *Acta Botanica Hungarica*, 64, 451–454. Available from: <https://doi.org/10.1556/034.64.2022.3-4.14>
- Halassy, M., Singh, A.N., Szabó, R., Szili-Kovács, T., Szitár, K. & Török, K. (2016) The application of a filter-based assembly model to develop best practices for Pannonian sand grassland restoration. *Journal of Applied Ecology*, 53, 765–773. Available from: <https://doi.org/10.1111/1365-2664.12618>
- Hamilton, N.E. & Ferry, M. (2018) Ggtern: ternary diagrams using ggplot2. *Journal of Statistical Software*, 87, 1–17.
- Han, X., Huang, J. & Zang, R. (2021) Shifts in ecological strategy spectra of typical forest vegetation types across four climatic zones. *Scientific Reports*, 11, 14127. Available from: <https://doi.org/10.1038/s41598-021-93722-7>
- Ho, K.V., Süle, G., Kovács, B. & Erdős, L. (2024) Strong differences in microclimate among the habitats of a forest-steppe ecosystem. *Időjárás*, 128. Available from: <https://doi.org/10.28974/idojaras.2024.1>
- Hulvey, K.B. & Aigner, P.A. (2014) Using filter-based community assembly models to improve restoration outcomes. *Journal of Applied Ecology*, 51, 997–1005. Available from: <https://doi.org/10.1111/1365-2664.12275>
- Jaagus, J., Aasa, A., Aniskevich, S., Boincean, B., Bojariu, R., Briede, A. et al. (2022) Long-term changes in drought indices in eastern and Central Europe. *International Journal of Climatology*, 42, 225–249. Available from: <https://doi.org/10.1002/joc.7241>
- Keddy, P.A. (1992) Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science*, 3, 157–164. Available from: <https://doi.org/10.2307/3235676>
- Kelemen, A., Török, P., Valkó, O., Miglécz, T. & Tóthmérész, B. (2013) Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation Science*, 24, 1195–1203. Available from: <https://doi.org/10.1111/jvs.12027>
- Király, G. (2009) *Új magyar fűvészkönyv*. Jósavafő: Aggtelek National Park.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M. et al. (2008) The LEDA Traitbase: a database of life-history traits of the northwest European flora. *Journal of Ecology*, 96, 1266–1274. Available from: <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Lenth, R.V. (2022) *Emmeans: estimated marginal means, aka least-squares means*. Version 1.7.5. Available from: <https://CRAN.R-project.org/package=emmeans>.
- Lhotsky, B., Cseceserits, A., Kovács, B. & Botta-Dukát, Z. (2016a) New plant trait records of the Hungarian flora. *Acta Botanica Hungarica*, 58, 397–400. Available from: <https://doi.org/10.1556/abot.58.2016.3-4.8>
- Lhotsky, B., Kovács, B., Ónodi, G., Cseceserits, A., Rédei, T., Lengyel, A. et al. (2016b) Changes in assembly rules along a stress gradient from open dry grasslands to wetlands. *Journal of Ecology*, 104, 507–517. Available from: <https://doi.org/10.1111/1365-2745.12532>
- Li, Y. & Shipley, B. (2017) An experimental test of CSR theory using a globally calibrated ordination method. *PLoS One*, 12, e0175404. Available from: <https://doi.org/10.1371/journal.pone.0175404>
- Lüdecke, D., Ben-Shachar, M.S., Patil, I., Waggoner, P. & Makowski, D. (2021) Performance: an R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6, 3139.
- McIntosh-Buday, A., Sonkoly, J., Takács, A., Balogh, N., Kovacsics-Vári, G., Teleki, B. et al. (2022) New data of plant leaf traits from Central Europe. *Data in Brief*, 42, 108286. Available from: <https://doi.org/10.1016/j.dib.2022.108286>
- Menezes, B.S., Martins, F.R., Dantas Carvalho, E.C., Souza, B.C., Silveira, A.P., Loiola, M.I.B. et al. (2020) Assembly rules in a resource gradient: competition and abiotic filtering determine the structuring of plant communities in stressful environments. *PLoS One*, 15, e0230097. Available from: <https://doi.org/10.1371/journal.pone.0230097>
- Molnár, Z., Biró, M., Bartha, S. & Fekete, G. (2012) Past trends, present state and future prospects of Hungarian forest-steppes. In: Werger, M.J.A. & van Staalduinen, M.A. (Eds.) *Eurasian Steppes*. Berlin: Springer, pp. 209–252.
- Münkemüller, T., Gallien, L., Pollock, L.J., Barros, C., Carboni, M., Chalmandrier, L. et al. (2020) Dos and don'ts when inferring assembly rules from diversity patterns. *Global Ecology and Biogeography*, 29, 1212–1229. Available from: <https://doi.org/10.1111/geb.13098>
- Negreiros, D., Stradic, S.L., Fernandes, G.W. & Renno, H.C. (2014) CSR analysis of plant functional types in highly diverse tropical grasslands of harsh environments. *Plant Ecology*, 215, 379–388. Available from: <https://doi.org/10.1007/s11258-014-0302-6>
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R. et al. (2022) *Vegan: community ecology package*. Version 2.6-2. Available from: <https://CRAN.R-project.org/package=vegan>.
- Petraitis, P. (2013) *Multiple stable states in natural ecosystems*. Oxford: Oxford University Press.
- Pierce, S., Luzzaro, A., Caccianiga, M., Ceriani, R.M. & Cerabolini, B. (2007) Disturbance is the principal α -scale filter determining niche differentiation, coexistence and biodiversity in an alpine community. *Journal of Ecology*, 95, 698–706. Available from: <https://doi.org/10.1111/j.1365-2745.2007.01242.x>
- Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M. et al. (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, 31, 444–457. Available from: <https://doi.org/10.1111/1365-2435.12722>
- R Core Team. (2021) *R: a language and environment for statistical computing*. Available from: <https://cran.r-project.org/bin/windows/base/>

- Rosenfield, M.F., Müller, S.C. & Overbeck, G.E. (2019) Short gradient, but distinct plant strategies: the CSR scheme applied to subtropical forests. *Journal of Vegetation Science*, 30, 984–993. Available from: <https://doi.org/10.1111/jvs.12787>
- Sábitz, J., Pongrácz, R. & Bartholy, J. (2014) Estimated changes of drought tendency in the Carpathian Basin. *Hungarian Geographical Bulletin*, 63, 365–378. Available from: <https://doi.org/10.15201/hungeobull.63.4.1>
- Sonkoly, J., Tóth, E., Balogh, N., Balogh, L., Bartha, D., Bata, K. et al. (2023) PADAPT 1.0 – the Pannonian dataset of plant traits. *Scientific Data*, 10, 742. Available from: <https://doi.org/10.1038/s41597-023-02619-9>
- Temperton, V.M., Hobbs, R.J., Nuttle, T. & Halle, S. (2004) *Assembly rules and restoration ecology: bridging the gap between theory and practice*. Washington, DC: Island Press.
- Tölgyesi, C., Zalatnai, M., Erdős, L., Batori, Z., Hupp, N.R. & Körmöcz, L. (2016) Unexpected ecotone dynamics of a sand dune vegetation complex following water table decline. *Journal of Plant Ecology*, 9, 40–50. Available from: <https://doi.org/10.1093/jpe/rtv032>
- Várallyay, G. (1993) Soils in the region between the Rivers Danube and Tisza (Hungary). In: Szujkó-Lacza, J. & Kováts, D. (Eds.) *The flora of the Kiskunság National Park*. Hungarian Natural History Museum: Budapest, pp. 21–42.
- Yu, J., Hou, G., Zhou, T., Shi, P., Zong, N. & Sun, J. (2022) Variation of plant CSR strategies across a precipitation gradient in the alpine grasslands on the northern Tibet plateau. *Science of the Total Environment*, 838, 156512. Available from: <https://doi.org/10.1016/j.scitotenv.2022.156512>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. The 13 study sites used in this study with coordinates and elevation, and the distribution of relevés across plant communities and sites.

Appendix S2. Ternary plots of weighted mean values of CSR strategies with square-root-transformed cover scores for the eight vegetation types.

Appendix S3. Statistical results of the pairwise comparisons of unweighted components C, S, and R.

Appendix S4. Relationships between plot scores on the primary DCA ordination axis and each weighted strategy component using square root transformation of cover scores: (a) C; (b) S, and (c) R; *p*-value and adjusted *R*-squared were calculated using linear regression; Slope: the slope value of the regression line; blue line is the regression line, and the gray area around the line represents the 95% confidence interval. Box plots demonstrate the variability of each strategy component: (d) C, (e) S, and (f) R in the eight communities.

How to cite this article: Erdős, L., Ho, K.V., Bede-Fazekas, Á., Kröel-Dulay, G., Tölgyesi, C., Batori, Z. et al. (2024) Environmental filtering is the primary driver of community assembly in forest–grassland mosaics: A case study based on CSR strategies. *Journal of Vegetation Science*, 35, e13228. Available from: <https://doi.org/10.1111/jvs.13228>