# Final report

FK 134384

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From the project, 8 scientific articles have been published where the principal investigator is the firstor the last author (4 D1, 3 Q1 and 1 Q4), with a total impact factor of 31.6. An additional scientific article is currently under review. Also, three articles have been published with the co-authorship of the principal investigator. In addition, five conference abstract have also been published from the project. In the followings, I summaruse the main results of the project.

## MAIN RESULTS

### 1)

### Forest-grassland coexistence in the Eurasian forest-steppe

Erdős L., Török P., Veldman J. W., Bátori Z., Bede-Fazekas Á., Magnes M., Kröel-Dulay Gy., Tölgyesi Cs. (2022): How climate, topography, soils, herbivores, and fire control forest–grassland coexistence in the Eurasian forest-steppe. Biological Reviews 97: 2195-2208. (D1, IF: 10.0)

To explain how the permanent coexistence of forest and grassland is possible in the Eurasian forest-steppe, we reviewed the literature and developed a series of conceptual models based on forest and grassland vitality patterns. The 'Mean Climate Model' predicts a rather sharp forest-grassland boundary, with no mosaic. The 'Zonal Model' also considers interannual climate variations, and predicts a narrow zone where patches of forests alternate with grasslands, but neither can gain a competitive advantage above the other for a sufficiently long period. In the 'Climatic-Topographic-Edaphic Model,' slope, aspect, and soils expand the ranges of the forest-grassland mosaic with local reversals of forest and grassland vitality relationships. The 'Climatic-Topographic-Edaphic-Herbivore-Fire Model' further extends the forest-steppe zone towards the north, where forests would dominate but are limited by fires and herbivores (Fig. 1). Feedbacks between the vegetation and the environment tend to stabilise existng forest-grassland patterns.

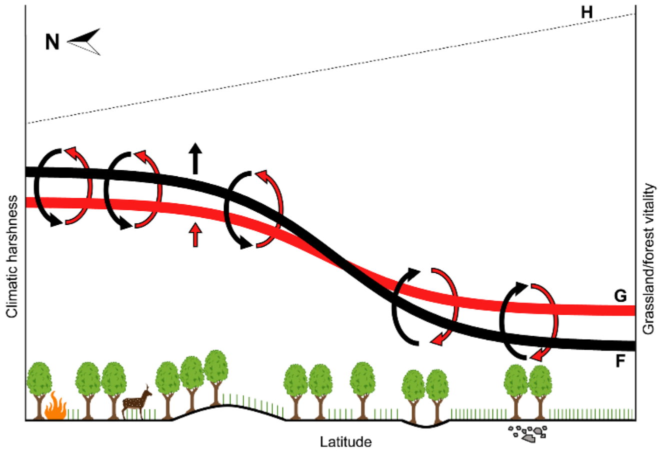

*Fig. 1. The 'Climatic-Topographic-Edaphic-Herbivore-Fire Model' of forest-grassland coexistence along a gradient of environmental harshness (H).. Circular arrows show how forest and grassland vitality (F and G, respectively) change locally as a result of topography, soil, fire, and herbivores.*

## 2) Patterns of taxonomic, functional, and phylogenetic diversity in Pannonian sandy forest-steppes

Erdős L., Ho K. V., Bátori Z., Kröel-Dulay Gy., Ónodi G., Tölgyesi Cs., Török P., Lengyel A. (2023): Taxonomic, functional, and phylogenetic diversity peaks do not coincide along a compositional gradient in forest-grassland mosaics. Journal of Ecology 111: 182–197. (D1, IF: 5.3)

We investigated the eight main habitats of Hungarian forest-grassland mosaics: large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands. There was a clear compositional gradient ranging from large forest patches through smaller-sized forest patches and edges to closed and open grasslands. In line with the edge-effect hypothesis, species richness peaked at the middle of the gradient (at edges) (Fig. 2a). Shannon diversity was high near the middle and at the open end of the gradient (Fig 2b). Functional diversity was high throughout woody habitats (in forests and at edges) and was significantly lower (Fig. 2c) in grasslands, probably reflecting different community assembly processes in these habitats. When considering all species, phylogenetic diversity tended to peak at north-facing forest edges (Fig. 2d), which was likely due to *Juniperus communis*, a species that prefers edges and smaller forest patches, wher it receives ample light. When excluding non-angiosperms, this peak in phylogenetic diversity at the edges disappeared (Fig. 2e). Differences of phylogenetic diversity between woody and grassland habitats may be explained by their different evolutionary ages.

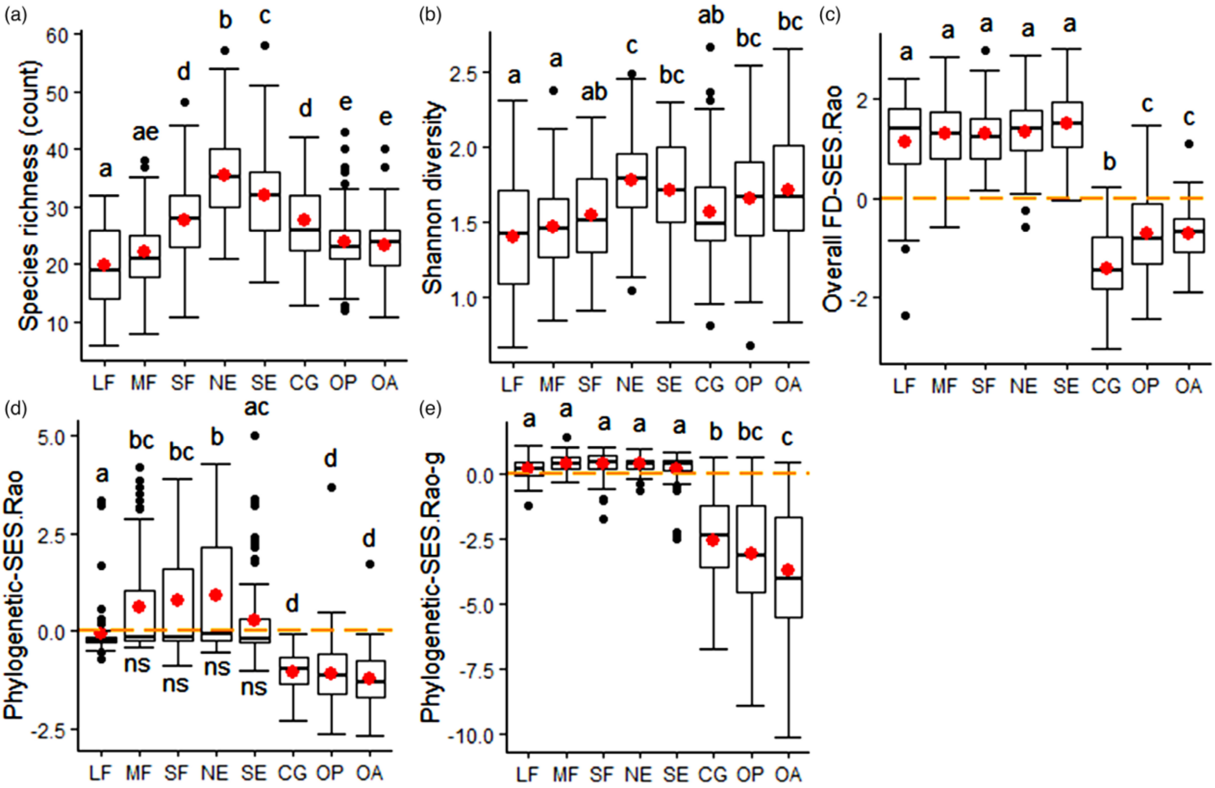

*Fig. 2. Patterns of (a) species richness, (b) Shannon diversity, (c) functional diversity, (d) phylogenetic diversity, and (e) phylogenetic diversity with angiosperms only. SES.RaoQ: Rao's quadratic entropy; LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; CG: closed perennial grasslands; OP: open perennial grasslands; OA: open annual grasslands.*

## 3) Plant strategies and community assembly in sandy forest-steppes

Erdős L., Ho K. V., Bede-Fazekas Á., Kröel-Dulay G., Tölgyesi C., Bátori Z., Török P. (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. (Q1, IF$_{2023}$: 2.2)

We studied eight vegetation types of Hungarian forest-steppes: large forest patches, medium forest patches, small forest patches, north-facing forest edges, south-facing forest edges, closed perennial grasslands, open perennial grasslands, and open annual grasslands. The trade-off between three key traits 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. Each vegetation type was dominated by the stress-tolerator strategy, indicating the prominent role of environmental filtering in community assembly. However, marked differences were found among the vegetation types regarding ecological strategies (Fig. 3): for example, the importance of the competitor strategy increased from grasslands to forests. The ruderal strategy was the most prominent in the open grasslands.

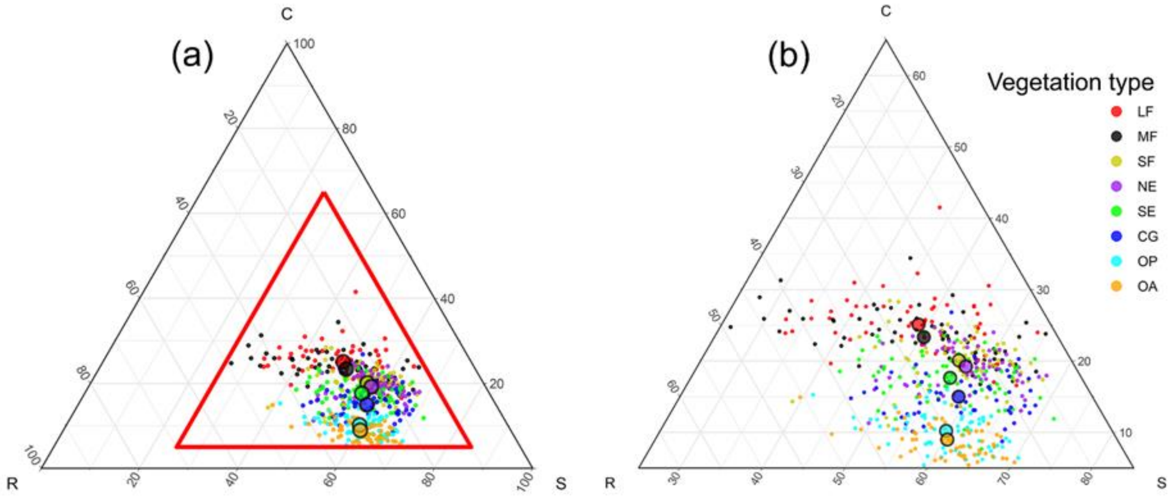

*Fig. 3. Ternary plots showing unweighted mean values of CSR strategies for the eight vegetation types. The red triangle in plot (a) shows the boundaries of plot (b). Larger symbols indicate the mean value for each vegetation type. LF: large forest patches; MF: medium forest patches; SF: small forest patches; NE: north-facing forest edges; SE: south-facing forest edges; CG: closed perennial grasslands; OP: open perennial grasslands; OA: open annual grasslands.*

## 4) Microclimate patterns in a sandy forest-steppe

Ho K. V., Süle G., Kovács B., Erdős L. (2024): Strong differences in microclimate among the habitats of a forest-steppe ecosystem. Időjárás 128: 1-26. (Q4, IF$_{2023}$: 0.8)

We characterised the microclimatic conditions of various forest-steppe habitats with repeated 24-h measurements throughout the growing season, using wireless sensors that recorded air temperature and air humidity values. As expected, open grasslands were the warmest and driest habitats. Among woody habitats, south-facing edges had the harshest microclimatic conditions. Surprisingly, we found that small forest patches and larger forest patches had similar air temperature and humidity variables, suggesting that even small groups of trees are able to lessen climatic harshness in forest-steppe ecosystems. With ongoing climate change, this role of forest patches is expected to become increasingly important.

## 5) The ecological and conservation value of near-natural forests and various tree plantations

Ho K. V., Kröel-Dulay Gy., Tölgyesi Cs., Bátori Z., Tanács E., Kertész M., Török P., Erdős L. (2023): Non-native tree plantations are weak substitutes for near-natural forests regarding plant diversity and ecological value. Forest Ecology and Management 531, 120789. (D1, IF: 3.7)

We compared near-natural poplar forests and the three most common tree plantation types (native deciduous *Populus alba*, non-native evergreen *Pinus nigra*, and non-native deciduous *Robinia pseudoacacia* plantations) in the Kiskunság Sand Ridge. The four habitat types proved to have significantly different species compositions. Although each habitat contained some diagnostic species, near-natural forests had the highest number of diagnostic species, mostly native shrubs. In contrast, tree plantations had many weeds and non-native herbs as diagnostic species. Near-natural forests contained the most species of high conservation importance (protected, endemic, and red-listed species). Near-natural forests had the highest per plot richness of native species (Fig. 4a) and the lowest richness of non-natives (Fig. 4b). Shannon diversity and functional diversity were higher in the near-natural forests and two types of plantations (*Populus* and *Pinus*) compared to *Robinia* plantations (Fig. 4c-d). Near-natural forests had the highest and *Robinia* plantations the lowest phylogenetic diversity (Fig. 4e). Based on naturalness indicator values, near-natural forests were the least degraded and *Robinia* plantations were the most degraded (Fig. 4f).

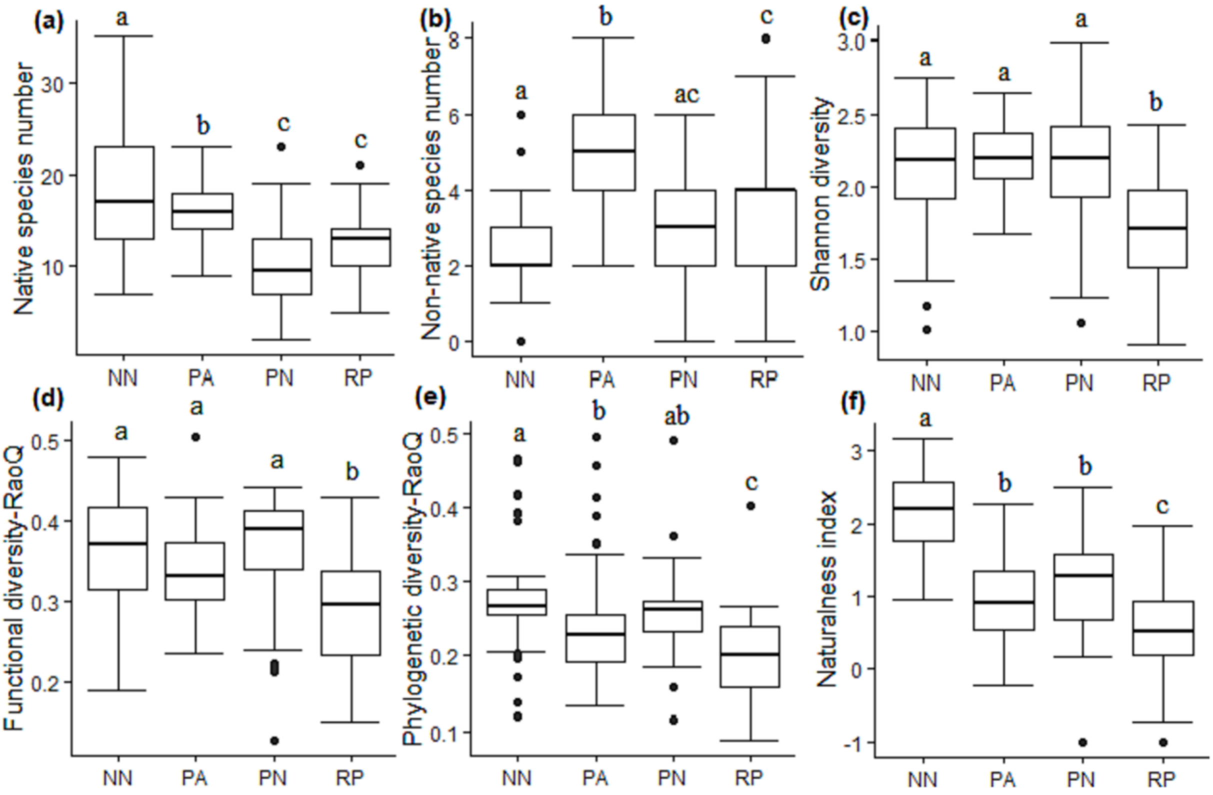

*Fig. 4. (a) The number of native species, (b) the number of non-native species, (c) Shannon diversity, (d) functional diversity, (e) phylogenetic diversity, and (f) the mean naturalness values of the four habitat types. NN: near-natural Populus alba forests. PA: plantations of the native Populus alba; PN: plantations of the non-native Pinus nigra; RP: plantations of the non-native Robinia pseudoacacia.*

## 6) Regional differences between the diversity patterns of sandy forest-steppes

Ho K. V., Ćuk M., Šikuljak T., Kröel-Dulay Gy., Bátori Z., Tölgyesi Cs., Fűrész A., Török P., Hábenczyus A. A., Hegyesi A., Coşgun L. Z., Erdős L. (2023): Forest edges revisited: species composition, edge-related species, taxonomic, functional, and phylogenetic diversity. Global Ecology and Conservation 46: e02625. (Q1, IF: 3.5)

We studied the species composition as well as taxonomic, functional, and phylogenetic diversity of four habitats (forest interior, north-facing forest edge, south-facing forest edge, and grassland in forest-grassland mosaics in the Kiskunság Sand Ridge (Hungary) and the Deliblato Sands (Serbia). The species composition of edges was significantly different from that of forests and grasslands, and included species that were rare or absent in habitat interiors (i.e., edge-related species). In the Kiskunság, species richness and Shannon diversity were generally higher at edges than in forest interiors and grasslands (Fig. 5a, b), which seems to confirm the edge-effect hypothesis. In contrast, in the Deliblato, edges were taxonomically not more diverse than grasslands (Fig. 5a, b), which contradicts the hypothesis. In the Kiskunság, forests and edges had higher functional diversity than grasslands, while there were no significant differences among the habitats in the Deliblato (Fig. 5c). The patterns found in the Deliblato clearly contradict the stress-dominance hypothesis. Based ont he analysis of functional diversity of single traits, it seems that functional diversity is strongly influenced by canopy openness and the traits of the dominant species. The open forest canopy in the Kiskunság results in high functional diversity for some traits such as life form and plant height, while the closed forest canopy in the Deliblato causes lower functional diversity. The phylogenetic diversity of woody habitats is higher than that of the grasslands (Fig. 5d, e).

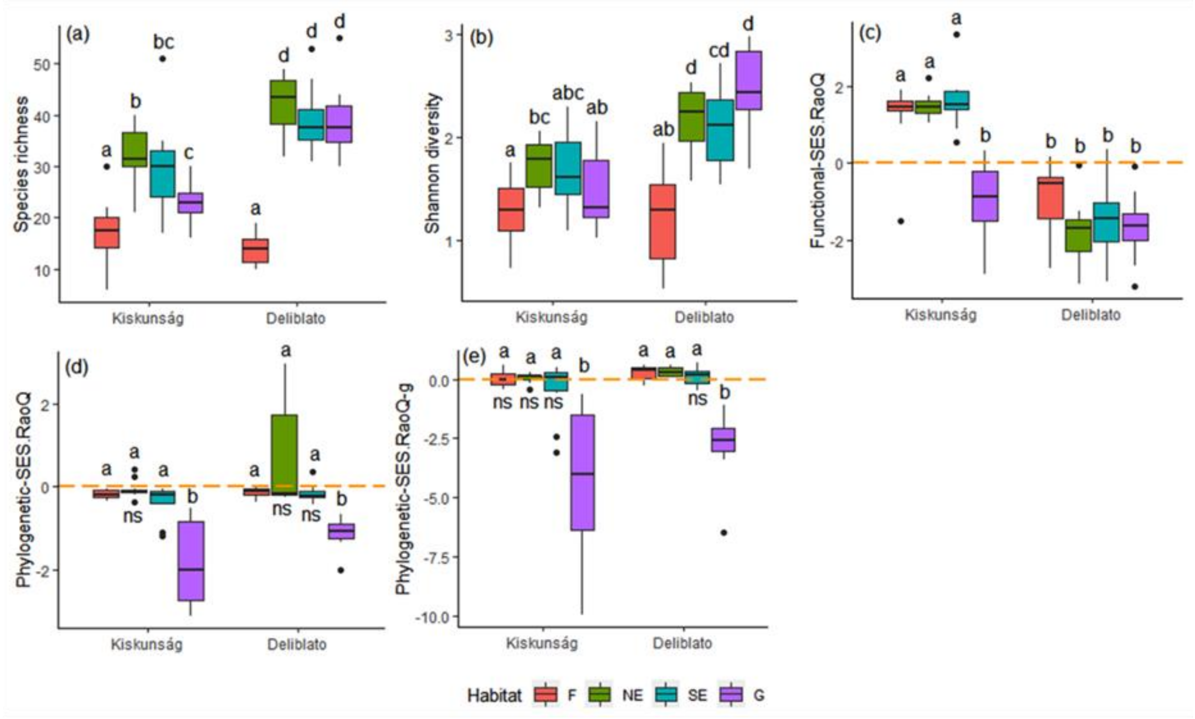

*Fig. 5. (a) Species richness, (b) Shannon diversity, (c) functional diversity, (d) phylogenetic diversity of all species, and (e) phylogenetic diversity of angiosperms only in the four habitat types in the Kiskunság and the Deliblato. SES.RaoQ: standardised effect size of Rao's quadratic; F: forest; NE: north-facing edge; SE: south-facing edge; G: grassland.*

## 7) A continental-scale cimate analysis of the forest-steppe zone

Bede-Fazekas Á., Török P., Erdős L. (2023): Empirical delineation of the forest-steppe zone is supported by macroclimate. Scientific Reports 13: 17379. (D1, IF: 3.8)

By conducting predictive distribution modeling and hierarchical clustering, we compared an earlier expert delineation of the forest-steppe zone and its regions (Erdős et al. Applied Vegetation Science 21: 345-362.) with the solely macroclimate-based predictions and clusters. Also, we identified the most important variables for predicting the Eurasian forest-steppe zone and its regions. The predicted probability of forest-steppe occurrence showed a very high agreement with the expert delineation. The previous delineation of the forest-steppe regions was only partly supported by this analysis. For example, the Far East region may be subdivided into three parts (Fig. 6).

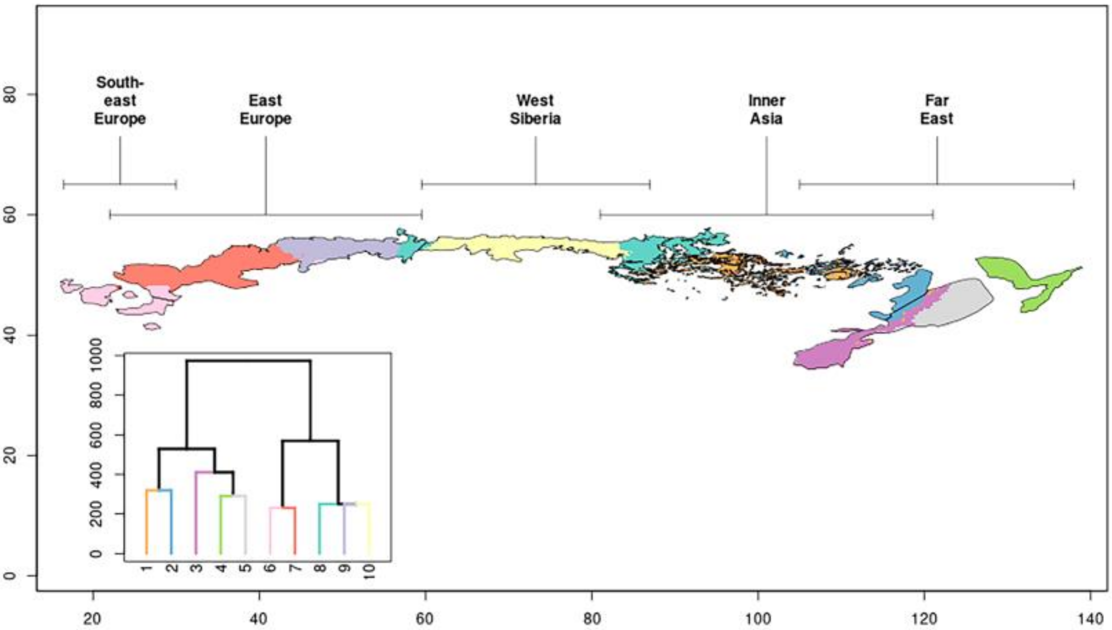

*Fig. 6. Result of the hierarchical clustering of the forest-steppe zone into ten clusters (inset in the bottom left corner) achieved on twenty macroclimatic variables, and the distribution of these clusters in the geographic space (main figure). The colors of the main figure and the subfigure match. Regions originally delineated by Erdős et al. but not used as input by the clustering are labeled and displayed with solid black lines for comparison.*

## 8) Sandy grassland dynamics in the Kiskunság

Erdős L., Ónodi G., Ho K. V., Tanács E., Akinyi R. Q., Török P., Tölgyesi Cs., Bátori Z., Kröel-Dulay Gy.: Between-year weather difference and long-term environmental trends both contribute to observed vegetation changes in a plot resurvey study. Ecology and Evolution 14: e70244. (Q1, IF$_{2023}$: 2.3)

We studied how the species composition and species richness of dry grasslands changed over a period of 17 years. All analyses were repeated after the removal of the spring ephemeral species from the datasat to analyse how the presence of spring ephemerals, which may react to short-term weather fluctuations rather than long-term climatic trends, may influence the results. Our findings demonstrate that the short-term fluctuation of spring ephemerals as a response to weather variability may have a considerable effect on the changes detected by plot resurveys. We found clearly identifyable species compositional changes between the two years, but the changes were less obvious when spring ephemerals were excluded. The significant increase in mean indicator values for temperatures, both with and without spring ephemerals, suggests that vegetation is already reacting to the increasing temperature. On the other hand, the apparent decrease in soil moisture values (when all species were analysed) disappeared when ephemerals were excluded, emphasising that fluctuations of spring ephemerals may indeed have a confounding effect on plot resurvey results. The observed changes in ecological indicator values without spring ephemerals (increasing temperature values and no change in moisture values) is in line with the observed climatic trends in the region. The observed decrease in per-plot species richness disappeared when spring ephemerals were excluded.

### 9) Forest-grassland heterogeneity at a decadal time scale

Erdős L., Ónodi G., Tölgyesi Cs., Kröel-Dulay Gy., Bátori Z., Aradi E., Török P., Ho K. V., Puspitasari I., Körmöczi L.: Forest encroachment in Eastern European forest-steppes at a decadal time scale (under review)

In this study we examined how the spatial heterogeneity of forest-steppes changes in time. We selected four study sites in the Kiskunság Sand Ridge, for which sites the land-use history is known in detail for the last couple of decades. Then we searched archive and recent photographs, and used a 1 ha square grid to split the sites into 1 ha units. Units that were affected by human intervention (forestry, invasive tree removal, etc.) were excluded from the analyses. From the remaining cells, random samples were taken and the area covered by forest was compared between the archive and the recent photographs. We found that the area of forest patches increased in all four sites significantly, despite the increasing temperature observed in the region. We propose that the change is the effect of grazing abandonment: grazing restricted the extension of forests, but after this activity reduced or ceased in the 20th century, forests started to expand. The number of forest patches significantly increased at one site, while it decreased at two sites and showed no significant change at the fourth site. This indicates that forest encroachment can happen at least in two different ways: through the emergence of new forest patches in the grassland, and through the extension and coalescence of already existing forest patches.

### 10) The ecological effects of tree plantations in the Danube-Tisza Interfluve

Tölgyesi Cs., Bátori Z., Deák B., Erdős L., Hábenczyus A. A., Kukla L. S., Török P., Valkó O., Kelemen A. (2021): A homokfásítás alkonya és az ártérfásítás hajnala. Természetvédelmi Közlemények 27: 126-144.

In this review paper, based on our earlier studies and a thorough literature review we evaluate the ecological role of tree plantations in the Danube-Tisza Interfluve. We conclude that afforestation does more harm than good in the region, and, consequently, it should be abandoned.