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The importance of forest patches in supporting steppe-species: a case study from the Carpathian Basin

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ABSTRACT

Moderating effects of trees on the environment in their immediate proximity are considered an important force in structuring plant communities, especially in harsh environments. In the semi-arid regions of the middle Carpathian Basin, such facilitative influences are expected to become crucial for the survival of several plant species, given the current warming and drying tendencies. We used 20 × 20 m plots to analyze whether grassland species adapted to mesic conditions penetrate forest patches, where they are able to survive. Using transects and the moving split window analysis, we also investigated how far the positive effects of the forest patches extend into grasslands, and whether this enables the existence of a steppe community that cannot tolerate extreme dry conditions and unfavorable soils. We found that beside forest-related species, forest patches hosted large numbers of grassland-related species. Among them, plants of closed steppe grasslands were the most numerous, which usually cannot tolerate the harsh conditions of open sandy grasslands, and are often confined to areas with better water and soil conditions. Our results showed that there is a 5–8 m wide closed steppe zone around the forest patches. Some species that are not able to survive in open xeric sandy grasslands are restricted to this zone. Unfortunately, while considerable attention is paid to the research, protection and restoration of sandy grasslands, forest patches are usually neglected. Our results emphasize that the establishment of individual trees and groups of trees should be actively promoted, because they have considerable nature conservation benefits by supporing closed steppe species.

INTRODUCTION

It is well-known that some species alter their physical environment so that they favor some species in their immediate proximity, a phenomenon often termed facilitation (van Andel 2005, Bronstein 2009, Mittelbach 2012). One of the best-known examples is that the canopy of certain trees may provide a suitable microclimate for other plants (Bruno et al. 2003, Brooker et al. 2008). In some cases, whole communities can form because of a facilitator species (Mittelbach 2012). Facilitation is thought to be most pronounced in harsh habitats, where extreme stress can be reduced by the facilitator species (Bertness and Callaway 1994, Callaway and Walker 1997, Brooker and Callaghan 1998). For example, several studies suggest that facilitation is especially important in dry habitats (Holmgren et al. 1997). In a sand-dune area, De Jong and Klinkhamer (1988) experimentally demonstrated that facilitative effects become stronger as water availability decreases. Similarly, trees seem to have a greater positive impact on the herb layer in xeric savannas than in savannas with higher rainfall (Belsky et al. 1993). The results of Tewksbury and Lloyd (2001) also showed that the canopy of the very same tree in the Sonoran Desert had a stronger facilitative effect in xeric sites than in less xeric ones.

The middle area of the Carpathian Basin, called Kiskunság Sand Ridge, has rather harsh environmental characteristics with a semiarid climate (Borhidi 1993) and soils with an extremely low water retention capacity (Bodrogközy 1982). The natural vegetation of the region is a mosaic, where open xeric grasslands and small xeric forest patches dominate,

while closed steppe grasslands appear mainly in the lowest-lying depressions and on more favorable soils. Under such circumstances, forest patches can be assumed to play an important role in providing suitable micro-habitats for certain species that would otherwise not be able to survive given the hot and dry conditions. Kovács-Láng et al. (2000) and Bartha et al. (2008, 2011) suggested that forest patches provide refuges for grassland species during severe droughts, may lessen the effects of increasing aridity due to climate change and are capable of promoting the regeneration of grasslands after disturbance events, although no detailed analyses have been carried out so far on this topic.

During the last 100 years, the temperature of the Carpathian Basin has increased, while precipitation has decreased considerably, and serious droughts have become more frequent (Kertész and Mika 1999, Zsákovics *et al.* 2007, Pálfai 2011). To make things worse, groundwater level has dropped by approximately 2 m in our study area since the 1980s, probably due to draining canals, afforestation and irrigation (Szalai 2011). This drying tendency is expected to continue (Bartholy *et al.* 2007, Pálfai 2011). As a consequence, the importance of the positive effects of native forest patches on their immediate surroundings may become greater.

However, the possibility of facilitation decreases as native forest patches are cleared. Paleoecological evidence shows that the forest component of the forest-steppe suffered great losses as a result of human activity from ca 3000 years BP (Magyari et al. 2010). Historical data suggest that deforestation was most severe between the 15th and the 19th centuries (Erdős et al. in press). Although some of the forest patches have recovered during the last 200 years, their potential nature conservation importance has not yet been fully recognized. Most of the ecological researches and the habitat-restoration measures have focused on grasslands (e.g. Margóczi et al. 1997, 2009, Halassy 2001, Horváth et al. 2009), while the significance of the sandy forest patches is usually under-rated (for an exception, see Molnár 1998). Based on the above considerations about the possible facilitative effects, the lack of forest patches in the landscape can have negative influences on

the grasslands, thus more attention should be paid on this issue.

The first aim of this study was to give a coenological characterization of the forest patches, with special regard to the species of the herb layer. We aimed to analyze the role of forest interiors in supporting some closed steppe plants which are unable to survive in the open xeric grasslands. Our second objective was to determine whether the positive effect of forest patches extends into grasslands. It is conceivable that some plants with higher moisture- and lower temperature requirements can occur in a band around the forests. We also aimed to find out how wide this zone can be, if it exists.

STUDY AREA

For our study, we chose a wooded-steppe fragment in South Hungary, near Ásotthalom (N46°12′, E19°47′) (Fig. 1a). The area is one of the oldest nature reserves in Hungary, protected since 1908, where no grazing and no forestry has been allowed for more than 100 years (Bodrogközy 1957, Gaskó 2009). The climate is semiarid: mean annual temperature is 10.6°C and mean annual precipitation is 580 mm (Ambrózy and Kozma 1990). The bedrock is sand.

The vegetation (Fig. 1b) consists of a mosaic of forest patches (Populo canescenti-Quercetum roboris) and open xeric grasslands (mainly Festucetum vaginatae) (Bodrogközy 1957). The size of the forest patches varies between a few tens of square meters (one or a few trees) to ca 1.5 ha. Their shape is mostly close to isodiametric. The canopy has a cover of 50–60%, and is dominated by silver and grey poplar trees (Populus alba L., $P. \times$ canescens (Ait.) Sm.). In the shrub layer, Berberis vulgaris L., Crataegus monogyna Jacq. and Ligustrum vulgare L. are the dominant species. The herb layer usually has a low vegetation cover, although cover values are higher in openings and along edges. Typical species include, among others, Cephalanthera rubra (L.) Rich., Elymus hispidus (Opiz) Melderis, *Epipactis atrorubens* Hoffm. ex Bess., Geum urbanum L., Hedera helix L. and Ranunculus polyanthemos L.

Grasslands between the forest patches are dominated by *Festuca vaginata* W. et K. and

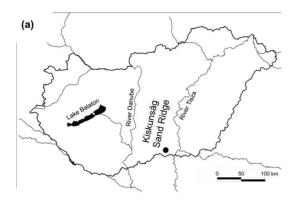




Fig. 1. (a) Location of the study area (black dot) in Hungary. (b) Typical forest patch situated in an open xeric sandy grassland.

Stipa borysthenica Klokov. Vegetation cover is extremely low (ca 30–50%), and patches of vascular plants alternate with mosses, lichens and bare soil. This unique community supports some valuable endemic plants such as Colchicum arenarium W. et K., Dianthus giganteiformis Borb. ssp. pontederae (Kern.) Soó, D. diutinus Kit., Iris humilis Georgi ssp. arenaria (W. et K.) A. et D. Löve.

MATERIAL AND METHODS

Field studies

To characterize the species composition of the forest patches, 15 forest patches (ca 0.1–1.5 ha) were selected, and one 20 × 20 m study plot was established randomly in each forest patch.

To analyze the influence of the forest patches on the neighboring grasslands, two forest stands were selected, their size being *ca* 0.5 ha and 0.8 ha. For both patches, one tran-

sect was designated, running from the forest interior through the edge into the grassland. The transects were north-facing, and consisted of 80 contiguous plots, 0.5×0.5 m each (thus the transects were 0.5 m wide and 40 m long).

Coenological relevés were made in both the large $(20 \times 20 \text{ m})$ and the small $(0.5 \times 0.5 \text{ m})$ plots, during which the percentage cover of all vascular plant species of the herb layer was estimated visually in April and July 2014. Spring and summer records were combined before analyses.

Data analyses

Species of the large plots were characterized according to their coenological preferences, based on the works of Soó (1980) and Borhidi (1995). All species were classified into one of the following categories: (1) forest-related species, (2) species of closed steppes, (3) species of open xeric sandy grasslands, (4) plants ocurring mainly in disturbed habitats, (5) indifferent species (*i.e.* species preferring more than one of the above categories). Species number per plot was calculated for each category, and results were displayed in boxplots, using SPSS 11.5.

To determine how far the effect of the forest extends into the grassland, the moving split window (MSW) analysis was used (Webster and Wong 1969). This method compares neighboring segments using a dissimilarity function, enabling the exact and objective identification of the boundary positions. The Squared Euclidean Distance (SED) was applied as comparative function, since it has been shown to efficiently detect vegetation boundaries in several studies (Erdős et al. 2014a). Significance of the boundaries was tested with the Z-score transformation. Overall mean and standard deviation were computed from 1000 randomizations and for the whole transect. Random reference was made with random shift. To reduce scaledependency, usually several window-widths are applied in MSW-studies (Erdős et al. 2014a). In the present study, we used window widths 2–20. For the final MSW-results, Zscores were averaged over all window widths. Average Z-scores were plotted against window midpoint position, resulting in a Z-score

profile. In the profile, possible vegetation boundaries appear as peaks; significant peaks are those which extend above z = 1.85 (Erdős et al. 2014b). Former studies have shown that MSW-peaks should be treated with care since some of them may indicate boundaries that are statistically significant but ecologically unimportant (Choesin and Boerner 2002). Therefore, after the analyses, results of the MSW were evaluated during an additional field survey.

Species' distributions along the interioredge-exterior gradient were visualized, taking into account only the presence and the absence of the species in the individual plots. Along both transects, three sections were identified (forest, transitional zone, open xeric grassland). We aimed to find out whether there are species that favor the transitional zone. Therefore, we identified diagnostic species of this zone, *i.e.* species that concentrate in one unit, whereas they are absent or rare in other units. For this purpose, phi-values were computed as indicators of fidelity (Tichý and Chytrý 2006), comparing observed species frequencies within this zone with frequencies that would be expected if the species were randomly distributed along the transect (cf.

Chytrý et al. 2002). Only diagnostic species having a phi value ≥ 0.500 were considered. We excluded non-significant diagnostic species with Fisher's exact test. Analyses were done with JUICE 7.0 (Tichý 2002).

To assess the environmental parameters along the transects, we used the ecological indicator values of Borhidi (1995). It has been shown that ecological indicators correlate well with measured parameters (e.g. Barczi et al. 1997), and they proved useful for studies along interior-edge-exterior gradients in sandy forest-steppes (Erdős et al. 2013). We calculated the frequency of the different indicator value categories in each plot along the transects, and performed MSW analyses for temperature, moisture and light values with the layouts described above.

RESULTS

In the 15 large relevés, a total of 100 vascular plant species have been recorded. Within each relevé, the number of forest-related species was always high (Fig. 2). Similarly, species of closed steppe grasslands, species of disturbed habitats, and species withouth a

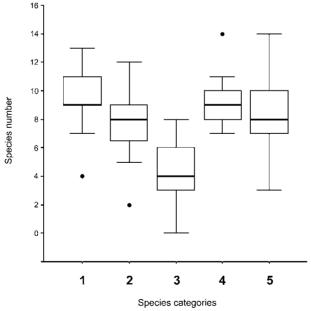


Fig. 2. Species numbers per plot for the five coenological preference categories. The boxes show the 25-75 percent quartiles, horizontal lines within the boxes represent medians. Whiskers indicate the highest and lowest values that are within the 1.5-times range of the box. Dots represent outliers. Categories are as follows: 1 – forest-related species, 2 – species of closed steppe grasslands, 3 – species of open xeric sandy grasslands, 4 – species of disturbed habitats, 5 – indifferent species (typical of more than one of the above categories)

| Table 1. Phi values and significance levels of the diagnostic species of the transitional closed steppe |
|--|
| grassland zone in the two transects. Phi values range between -1 and +1; high values show that the spe- |
| cies is concentrated in the given vegetation unit, and is rare or totally absent elsewhere. Only species |
| with phi values ≥ 0.500 are shown. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$. |

| Species name | transect 1 | transect 2 |
|------------------------|------------|------------|
| Asperula cynanchyca | - | 0.506** |
| Bromus sterilis | - | 0.618*** |
| Calamagrostis epigeios | 0.503* | 0.636*** |
| Carex liparicarpos | 0.540** | - |
| Dianthus pontederae | - | 0.541*** |
| Falcaria vulgaris | 0.703*** | - |
| Festuca rupicola | 0.719*** | - |
| Galium verum | - | 0.731*** |
| Medicago falcata | 0.863*** | 0.814*** |
| Pimpinella saxifraga | 0.500* | |
| Poa angustifolia | 0.726*** | 0.684*** |
| Seseli annuum | 0.796*** | 0.520** |
| Teucrium chamaedrys | 0.850*** | - |

clear coenological preference were also numerous. In contrast, species of open xeric sandy grasslands were less frequent.

In the 160 small plots, we found a total of 76 vascular plant species. 61 species occurred along transect 1, and 58 species along transect 2. The MSW analysis identified one significant boundary along transect 1, between plots 45 and 46, corresponding to the boundary between a closed and an open grassland (Fig. 3b). An almost significant peak emerged between plots 40 and 41. This peak was regarded as indicating the boundary between the forest and the neighboring closed grassland. Further non-significant peaks appeared within the open grassland, indicating compositional changes due to the uneven relief. The closed grassland, as a transitional zone between the forest and the open sandy grassland, proved to be 5 m wide (Fig. 3b). The species' distribution patterns showed that there were some species apparently preferring this zone and its immediate surroundings (Fig. 3a).

The ecological indicator values showed that there were two major changes in environmental parameters along the transect (Fig. 3c). Temperature, moisture and light values showed a considerable change near the edge (but within the forest), and another change occurred at the boundary of the closed and the open grasslands. The frequencies of the temperature values had additional changes along the transect.

As for transect 2, the situation was a bit more complicated (Fig. 4b), with four significant peaks. The first one (between plots 42 and 43) corresponded to the boundary between the forest interior and a shrubby edge. The second peak indicated an additional transition where a change in both composition and abundance occurred. The third peak (between plots 50 and 51) indicated the boundary between the shrubby forest edge and the adjacent closed grassland. The fourth boundary (between plots 58 and 59) was situated between the closed grassland and the open sandy grassland. Here, the transitional closed grassland zone between the forest (including the shrubby edge) and the open sandy grassland was 8 m wide (Fig. 4b). On the graph depicting species' distribution patterns, it is obvious that some species seem to prefer the zones of the shrubby edge and the closed grassland (Fig. 4a).

Environmental parameters proved to change at two locations along transect 2 (Fig. 4c). First, there were smaller changes within the forest, near the edge, and second, greater changes occurred at the closed grassland-open grassland interface.

We identified nine species diagnostic for the transitional closed grassland in transect 1, and eight in transect 2 (Table 1). The overlap was considerable, as four species were diagnostic for the transitional zone along both transects.

DISCUSSION AND CONCLUSIONS

As climatic parameters become more and more arid in the Carpathian Basin, especially in the Kiskunság Sand Ridge (e.g. Bartholy et al. 2007, Zsákovics et al. 2007), forest patches will become more important in supporting some mesic plant species. However, no studies have been conducted on this topic yet, and, as a result, the role of sandy forest patches in nature conservation is not fully appreciated during preservation and restoration projects.

Based on the large relevés, it can be concluded that forest patches provide habitats not only for typical forest-related species, but also for several grassland-related ones (Fig. 2). Thus, grassland-related plants can be found not only in forest edges (e.g. Molnár 2009), but some of them penetrate into forest interiors. Most of these grassland-related plants usually occur in closed steppes, where abiotic parameters are more favorable than in open sandy grasslands. However, if no such site is available, as is the case in our study area, closed steppe species are restricted to forests and their surroundings.

We identified a transitional zone between forests and open xeric sandy grasslands, with its own species composition (Table 1). It proved to be 5 m wide in transect 1 (Fig. 3), and 8 m wide in transect 2 (Fig. 4). As we see it, these zones around forest patches should

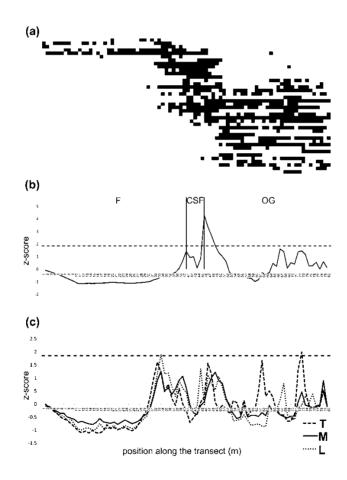


Fig. 3. (a) Species distribution patterns along transect 1. Rows represent species, columns show plots along the transect. Within each row, presence of the given species is displayed in black, absence in white. (b) Z-score (standardized Squared Euclidean Distance) profile of transect 1 for species cover values. The solid line shows the z-scores plotted against spatial position. The horizontal dashed line is the critical value (z = 1.85), above which peaks are significant. F – forest, CSF – closed steppe fragment, OG – open grassland. (c) Z-score profile of transect 2 for ecological indicator value frequencies. T – temperature, M – moisture, L – light intensity.

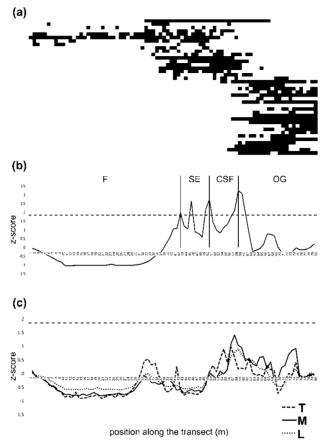


Fig. 4. (a) Species distribution patterns along transect 2. Rows represent species, columns show plots along the transect. Within each row, presence of the given species is displayed in black, absence in white. (b) Z-score (standardized Squared Euclidean Distance) profile of transect 2 for species cover values. The solid line shows the z-scores plotted against spatial position. The horizontal dashed line is the critical value (z = 1.85), above which peaks are significant. F – forest, SE – shrubby edge, CSF – closed steppe fragment, OG – open grassland. (c) Z-score profile of transect 2 for ecological indicator value frequencies. T – temperature, M – moisture, L – light intensity.

be viewed as fragments of the closed steppe grassland community Astragalo-Festucetum rupicolae (a description of the association is given by Borhidi et al. 2012). This community has a higher water demand than open xeric sandy grasslands, and it usually cannot tolerate extreme high temperatures (Bölöni et al. 2011). It has been suggested that similar steppe fragments around forests served as refuges for steppe species when most of the steppes were converted into arable fields (Molnár et al. 2008). At present, gradually drying conditions threaten the survival of steppe species. As a result, these plants depend on locally more favorable environments, which can emerge as a result of shading (Bölöni et al. 2011). Therefore, the nature conservation importance of forests will increase (also see Biró *et al.* 2008). Similarly, Frost and McDougald (1989) emphasized the role of trees during extreme droughts in Californian grasslands.

Erdős with co-authors (2014c) have shown that forest patches scattered in dry sandy grassland can significantly modify temperature and moisture values both within the forest stands and in the edge zones. Forests and edges are more humid and less warm during the day, with a considerably lower daily temperature variation range. Our present results reinforce these findings, and add some valuable new information. Earlier studies did not reveal where the environmental parameters start to change, and how far the

effect extends into grasslands. Our analysis of the ecological indicator values suggested that environmental parameters start to change within the forest interior, approaching to the edge. Also, there were obvious changes at the interface of closed and open grasslands, suggesting that forest patches exert a considerable influence on temperature, moisture and light values, and this influence extends up to 8 m into the grasslands.

It has to be noted that in most cases peaks in the MSW profile were not significant for the ecological indicator values (Figs 3c and 4c). It has been suggested by Diekmann (2003) that fine-scale differences are sometimes hard to detect using ecological indicator values. Although instrumental measurements could provide valuable data, we think that our analysis is valuable and shows clear trend even if most peaks are not significant.

It is well-known that differently oriented edges have different microclimatic and vegetation characteristics (e.g., Ries et al. 2004). Both of our transects in the present study were north-facing. Further studies are needed to determine how the survival of steppe species is affected in different expositions. For example, it is possible that the closed steppe fragment is narrower in southern expositions.

Forest patches situated in open xeric sandy grasslands have several advantages. They host some valuable forest-related species (Erdős *et al.* 2013), contribute to landscapescale heterogeneity, and sequestrate carbon dioxide.

The above considerations, together with the results of the present study have some profound nature conservation implications. Nowadays, sandy grassland restoration, maintenance, and the control of invasive species usually involves either grazing or mowing. However, we see that attention should be paid not to harm native tree seedlings and saplings so that they can become full-grown trees within a few decades. Moreover, planting trees would also be desirable in places where natural regeneration is too slow. Populus alba could be one of the most promising species, since it is native to the region, grows fast, and tolerates both sandy soils and xeric climatic conditions (Kopecky 1978, Bartha 1999; Rédei 2010). Protecting the existing forest patches, and promoting the establishment of new ones in xeric sandy grasslands would be a desirable step towards the original mosaic landscape of the region (Zólyomi 2007), and at the same time it would be beneficial for closed steppe species as well.

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REFERENCES

Ambrózy P., Kozma F. 1990 – [Climate of the Dorozsma-Majsa sand region] (In: [Cadaster of the Basic Landscape Units of Hungary I] Ed: S. Marosi, S. Somogyi) – MTA Földrajztudományi Kutató Intézet, Budapest, pp. 84–85 (in Hungarian).

Barczi A., Penksza K., Czinkota I., Néráth M. 1997

– A study of connection between certain phytoecological indicators and soil characteristics in the case of the Tihany peninsula – Acta Bot. Hung. 40: 1–14.

Bartha D. 1999 – [Tree and shrub species of Hungary] – Mezőgazda Kiadó, Budapest, 302 pp. (in Hungarian).

Bartha S., Campetella G., Kertész M., Hahn I., Kroel-Dulay Gy., Rédei T., Kun A., Virágh K., Fekete G., Kovács-Láng E. 2011 – Beta diversity and community differentiation in dry perennial sand grasslands – Ann. Bot. 1: 9–18.

Bartha S., Campetella G., Ruprecht E., Kun A., Házi J., Horváth A., Virágh K., Molnár Zs. 2008 – Will interannual variability in sand grassland communities increase with climate change? – Community Ecol. 9: 13–21.

Bartholy J., Pongrácz R., Gelybó Gy. 2007 – Regional climate change expected in Hungary for 2071–2100 – Appl. Ecol. Environ. Res. 5: 1–17.

Belsky A.J., Mwonga S.M., Amundson R.G., Duxbury J.M., Ali A.R. 1993 – Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas – J. Appl. Ecol. 30: 143–155.

Bertness M.D., Callaway R. 1994 – Positive interactions in communities – Trends Ecol. Evol. 9: 191–193.

Biró M., Révész A., Molnár Zs., Horváth F., Czúcz B. 2008 – Regional habitat pattern of the Danube-Tisza Interfluve in Hungary II – Acta Bot. Hung. 50: 19–60.

- Bodrogközy Gy. 1957 Die Vegetation der Weisspappel-Haine in dem Reservat Emlékerdő bei Szeged-Ásotthalom Acta Biol. Szeged. 3: 127–140.
- Bodrogközy Gy. 1982 Hydroecology of the vegetation of sandy forest-steppe character in the Emlékerdő at Ásotthalom Acta Biol. Szeged. 28: 13–39.
- Borhidi A. 1993 Characteristics of the climate of the Danube-Tisza Mid-region (In: The flora of the Kiskunság National Park I, Eds: J. Szujkó-Lacza, D. Kováts) – Hungarian Natural History Museum, Budapest, pp. 9–20.
- Borhidi A. 1995 Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian Flora Acta Bot. Hung. 39: 97–181.
- Borhidi A., Kevey B., Lendvai G. 2012 Plant communities of Hungary – Akadémiai Kiadó, Budapest, 544 pp.
- Bölöni J., Molnár Zs., Kun A. 2011 [Habitat types of Hungary] MTA ÖBKI, Vácrátót, 439 pp. (in Hungarian).
- Bronstein J.L. 2009 The evolution of facilitation and mutualism J. Ecol. 97: 1160–1170.
- Brooker R.W., Callaghan T.V. 1998 The balance between positive and negative plant interactions and its relationship to environmental gradients: a model Oikos, 81: 196–207.
- Brooker R.W., Maestre F.T., Callaway R.M., Lortie C.L., Cavieres L.A., Kunstler G., Liancourt P., Tielbörger K., Travis J.M.J., Anthelme F., Armas C., Coll L., Corcket E., Delzon S., Forey E., Kikvidze Z., Olofsson J., Pugnaire F., Quiroz C.L., Saccone P., Schiffers K., Seifan M., Touzard B., Michalet R. 2008 Facilitation in plant communities: the past, the present, and the future J. Ecol. 96: 18–34.
- Bruno J.F., Stachowicz J.J., Bertness M.D. 2003 Inclusion of facilitation into ecological theory Trends Ecol. Evol. 18: 119–125.
- Callaway R.M., Walker L.R. 1997 Competition and facilitation: a synthetic approach to interactions in plant communities Ecology, 78: 1958–1965.
- Choesin D., Boerner R.E.J. 2002 Vegetetation boundary detection: A comparison of two approaches applied to field data Plant Ecol. 158: 85–96.
- Chytrý M., Tichý L., Holt J., Botta-Dukát Z. 2002.
 Determination of diagnostic species with statistical fidelity measures J. Veg. Sci. 13: 79–90.
- De Jong T.J., Klinkhamer P.G.L. 1988 Seedling establishment of the biennials *Cirsium vulgare* and *Cynoglossum officinale* in a sand-dune area: the importance of water for differential survival and growth J. Ecol. 76: 393–402.

- Diekmann M. 2003 Species indicator values as an important tool in applied plant ecology: a review – Basic Appl. Ecol. 4: 493–506.
- Erdős L., Bátori Z., Tölgyesi Cs., Körmöczi L. 2014a – The moving split window (MSW) analysis in vegetation science: an overview – Appl. Ecol. Env. Res. 12: 787–805.
- Erdős L., Gallé R., Körmöczi L., Bátori Z. 2013 Species composition and diversity of natural forest edges: edge responses and local edge species Community Ecol. 14: 48–58.
- Erdős L., Tölgyesi Cs., Ćseh V., Tolnay D., Cserhalmi D., Körmöczi L., Gellény K., Bátori Z. Vegetation history, recent dynamics and future prospects of a Hungarian sandy forest-steppe reserve: forest-grassland relations, tree species composition and size-class distribution Community Ecol. (in press).
- Erdős L., Tölgyesi Cs., Horzse M., Tolnay D., Hurton Á., Schulcz N., Körmöczi L., Lengyel A., Bátori Z. 2014c Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications Ecol. Complex. 17: 107–118.
- Erdős L., Zalatnai M., Bátori Z., Körmöczi L. 2014b Transitions between community complexes: a case study analysing gradients through mountain ridges in South Hungary Acta Bot. Croat. 73: 63–77.
- Frost W.E., McDougald N.K. 1989 Tree canopy effects on herbaceous production of annual rangeland during drought J. Range Manage. 42: 281–283.
- Gaskó B. 2009 [On the conservation of the natural and near-natural habitats in Csongrád county] Stud. Nat. 5: 5–486 (in Hungarian, English summary).
- Halassy M. 2001 Possible role of the seed bank in the restoration of open sand grassland in old fields – Community Ecol. 2: 101–108.
- Holmgren M., Scheffer M., Huston M.A. 1997 The interplay of facilitation and competition in plant communities Ecology, 78: 1966–1975.
- Horváth A., Szemán L., Bartha S., Virágh K., Bölöni J., Fülöp Gy., Rév Sz. 2009 [Possibilities of restoration of natural or seminatural grasslands] Gyepgazdálkodási Közlem. 6: 19–27 (in Hungarian, English summary).
- Kertész A., Mika J. 1999 Aridification, climate change is South-eastern Europe Phys. Chem. Earth Pt. A. 24: 913–920.
- Kopecky F. 1978 [Common aspen and silver poplar] (In: [Poplar and willow plantations] Ed: B. Keresztesi) Mezőgazdasági Kiadó, Budapest, pp. 30–33 (in Hungarian).
- Kovács-Láng E., Kröel-Dulay Gy., Kertész M., Fekete G., Bartha S., Mika J., Dobi-Wantuch I., Rédei T., Rajkai K., Hahn I. 2000 – Changes

- in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change Phytocoenologia, 30: 385–407.
- Magyari E.K., Chapman J.C., Passnore D.G., Allen J.R.M., Huntley J.P., Huntley B. 2010 Holocene persistence of wooded steppe in the Great Hungarian Plain J. Biogeogr. 37: 915–935.
- Margóczi K., Fehér M., Hrtyan M., Gradzikiewicz M. 2009 [Evaluation of old-fields and ecological restoration of grasslands in the Great Hungarian Plain] Természetvédelmi Közlem. 15: 182–192 (in Hungarian, English summary).
- Margóczi K., Körmöczi L., Kincsek I. 1997 Regeneration of sand grasslands: case studies in two different scales ANP Füzetek 1: 233–239.
- Mittelbach G.G. 2012 Community ecology Sinauer Associates, Sunderland, 400 pp.
- Molnár Zs. 1998 Interpreting present vegetation features by landscape historical data: an example from a woodland-grassland mosaic landscape (Nagykőrös Wood, Kiskunság, Hungary) (In: The ecological history of European forests, Eds: K.J. Kirby, C. Watkins) CAB International, Wallingford, pp. 241–263.
- Molnár Zs. 2009 [The Holocene history of the vegetation types of the central part of the Great Hungarian Plain: a paleoecological review from a vegetation scientist's poin of view] Kanitzia, 16: 93–118 (in Hungarian, English summary).
- Molnár Zs., Fekete G., Biró M., Kun A. 2008 [Land-use history of the sandy steppes of the Danube-Tisza Interfluve] (In: [Soil-plant-climate interactions] Eds: Gy. Kröel-Dulay, T. Kalapos, A. Mojzes) MTA ÖBKI, Vácrátót, pp. 39–56 (in Hungarian).
- Pálfai I. 2011 [Extreme droughts ont he Hungarian Plain between 1931 and 2010] (In: [Environmental changes and the Hungarian plain], Ed: J. Rakonczai) Nagyalföld Alapítvány, Békéscsaba, pp. 87–96. (in Hungarian).

- Rédei K. 2010 [Forest plantations] Debreceni Egyetemi Kiadó, Debrecen, 88 pp. (in Hungarian).
- Ries L., Fletcher R.J., Battin J., Sisk T.D. 2004 Ecological responses to habitat edges: mechanisms, models, and variability explained Annu. Rev. Ecol. Evol. S. 35: 491–522.
- Soó R. 1980 [Reference book of the Hungarian flora and vegetation VI] Akadémiai Kiadó, Budapest, 556 pp. (in Hungarian).
- Szalai J. 2011 [Changes in water table depth int he Hungarian Plain] (In: [Environmental changes and the Hungarian Plain] Ed: J. Rakonczai) Nagyalföld Alapítvány, Békéscsaba, pp. 97–110 (in Hungarian).
- Tewksbury J.J., Lloyd J.D. 2001 Positive interactions under nurse-plants: Spatial scale, stress gradients and benefactor size Oecologia, 127: 425–434.
- Tichý L. 2002 JUICE, software for vegetation classification J. Veg. Sci. 13: 451–453.
- Tichý L., Chytrý M. 2006 Statistical determination of diagnostic species for site groups of unequal size J. Veg. Sci. 17: 809–818.
- van Andel J. 2005 Species interactions structuring plant communities (In: Vegetation ecology, Ed: E. van der Maarel) Blackwell, Malden, pp. 238–264.
- Webster R., Wong I.F.T. 1969 A numerical procedure for testing soil boundaries interpreted from air photographs Photogrammetria, 24: 59–72.
- Zólyomi B. 2007 [Natural vegetation of Hungary] (In: [Pannon encyclopedia: Flora and vegetation of Hungary] Ed: M. Járai-Komlódi) Urbis, Budapest, pp. 156–157 (in Hungarian).
- Zsákovics G., Kovács F., Kiss A., Pócsik E. 2007 Risk analysis of the aridification endangered sand-ridge area in the Danube-Tisza Interfluve Acta Climatol. Chorol. Univ. Szeged. 40–41: 169–178.