Species composition and diversity of natural forest edges: edge responses and local edge species

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Abstract: Habitat boundaries in general and forest edges in particular belong to the central issues in ecology. Theories about community and environmental edge-responses are diverse, but there is a lack of sufficient supporting field evidence: no consensus exists about distinctness and diversity of edges, and the existence of edge-related species. Moreover, as most studies focus on man-made edges, natural forest edges are less understood. We studied xeric forest edges in a wooded-steppe area. Twelve forest patches were selected, and plots were set up within the edges, the forest interiors and the grasslands. Species composition, species richness and Shannon diversity were compared between the three habitat types as well as between differently oriented edges. We identified diagnostic species for all habitats. Local habitat preferences of the edge-related species were compared to their regional preferences. Environmental factors of the different habitats were assessed by using ecological indicator values. Forest edges differed both from forest interiors and grasslands, forming a narrow but distinct habitat type between them. Species composition of the edges was not simply a mixture of forest and grassland species, but there were several edge-related species, most of which are regionally regarded as typical of closed steppe grasslands. Neither shady conditions of the forests, nor dry conditions of the grasslands are tolerated by these species; this is why they are confined to edges. Species richness and Shannon-diversity were higher within edges than in either of the habitat interiors. Ecological indicator values suggested that light intensity and temperature were higher in the edges than in the forests, but were lower than in the grasslands. In contrast, soil moisture was lower in the edges than in the forests but was higher than in the grasslands. There were slight differences between differently exposed edges concerning species composition, species richness and Shannon diversity. We conclude that edges should be considered an integral part of wooded-steppes. Their high diversity may have nature conservation implications. Our study emphasizes that edge species may be confined to edges only locally, but may have a broader distributional range in other areas. These species may be referred to as local edge species. Our results also point out that the very same edge can be interactive and non-interactive at the same time, depending on the characteristics considered.

Nomenclature: Simon (2000).

Introduction

Boundary zones are currently regarded as important components of heterogeneous areas (Cadenasso et al. 2003). They control the ecological flows between neighbouring patches (Wiens et al. 1985, Wiens 1992, Cadenasso et al. 2003), they affect within-patch dynamics (Fagan et al. 1999) and may play an important role in nature conservation (Kark and van Rensburg 2006, Yarrow and Marín 2007).

Forest edges belong to the most conspicuous boundary types, thus they have been extensively studied (cf. Harper et al. 2005). Species composition of forest edges may be similar to that of forest interiors (e.g. Jakucs 1972, Mészáros 1990, Orczewska and Glista 2005, Santos and Santos 2008), but different patterns also exist (Fraver 1994, Erdős et al. 2011), emphasizing that edges should not always be regarded as belonging to the forest stand. In fact, Central European botanists consider forest edges forming a separate unit between the two neighbouring communities, although their floristic distinctness is a disputed issue (Papp 2007).

One of the most controversial topics related to edge research is species diversity within edges. The most popular theory suggests that diversity is higher in edges than in patch interiors (e.g. Odum 1971, Risser 1995). Critics of this notion claim that diversity within edges depends on certain characteristics of the edge: sharp edges with fluctuating environmental conditions have lower diversity, while blurred and stable ones possess higher diversity than patch interiors do (van Leeuwen 1966, Brown and Gibson 1983, van der Maarel 1990). Smith (1992) hypothesized that the greater the contrast between two neighbouring habitats, the greater should the diversity be within the edge. As van der Maarel (1990) pointed out, diversity within edges may be intermediate between the two adjoining habitats. Results of field studies are often contradicting (Murcia 1995, Harper et al. 2005, Kark and van Rensburg 2006), thus no generalizations have been possible so far, which calls for more case studies.

Another hotly debated topic is the existence of edge-related species. Unfortunately, there is no consensus on how to define edge-related species (Lloyd et al. 2000): should an edge-related species occur exclusively within edges or is it

satisfactory when it is significantly more frequent in edges? Apart from the terminological difficulties, there is a limited number of field studies, and, in addition, some of them have contradictory results (Kark and van Rensburg 2006). Moreover, as Lloyd et al. (2000) pointed out, one should always be careful when evaluating results, since a species that seems to be confined to edges at one site may not be edge-related at another site.

Orientation of forest edges exerts a major impact on the microclimate (e.g., Young and Mitchell 1994, Gehlhausen et al. 2000), possibly influencing vegetation properties (Ries et al. 2004). Orientation of edges should be taken into account during studies on forest edges as disregarding edge orientation may contribute to the inconsistency among studies (Murcia 1995, Ries et al. 2004). Numerous studies have been conducted on differently exposed edges (e.g., Chen et al. 1993, Heithecker and Halpern 2007), yet more case studies are needed to disentangle the relationship between microclimatic conditions and vegetation features such as species composition and diversity.

It is important to make a distinction between naturally and anthropogenically fragmented habitats (Ewers and Didham 2006, Papp 2007). As man-made edges have received greater attention (Harper et al. 2005), natural edges are less understood. However, natural edges are of great importance in mosaic landscapes. The Great Hungarian Plain, belonging to the wooded-steppe zone (Borhidi 1961, Magyari et al. 2010), supports alternating forest and grassland patches of various sizes, forming a mosaic-like vegetation pattern (Wendelberger 1989, Kevey 2008). In the sandy ridge of the Danube-Tisza Interfluve, remnants of near-natural vegetation can still be found (Fekete et al. 2002). There have been no detailed studies concerning forest edges in this region. For our research, a nature reserve near Ásotthalom (southern Hungary) was chosen, where a small part of the wooded-steppe survived.

We assessed the species richness and Shannon-diversity of the edges and compared them to the forest interiors and grasslands. We also tried to identify species that are edge-re-

lated in this mosaic complex. Based on the most wide-spread theories on ecological edges, we hypothesized that edges might possess species from both habitat interiors, as well as their own species, resulting in an increased diversity and the formation of a distinct edge community.

Environmental variables (temperature, moisture and light intensity) of the edges were assessed using ecological indicator values. The canopy and the shrub layer above the edge provide shady conditions for certain periods of the day, probably affecting soil moisture and temperature. Therefore, intermediate values were expected within edges, compared to the interiors of the two adjoining habitats.

In this study, possible differences between south-oriented and north-oriented edges were also scrutinized. Our hypothesis was that south-facing edges would be warmer, dryer and less shady, resulting in a habitat less favourable for edge-related species. Therefore, species richness, diversity and the number of edge-related species were expected to be lower in south-facing edges than in north-facing ones.

Materials and methods

Study area

Our study was conducted in the Ásotthalom Nature Reserve (southeastern part of the Danube-Tisza Interfluve, Hungary) (Fig. 1a). Climate shows a clear semiarid character (Borhidi1993) with a mean annual temperature of 10.6°C (Ambrózy and Kozma 1990) and a mean annual precipitation of 572 mm (Fröhlich in Gaskó 2009). The area is characterized by small sand dunes. Grasslands grow on humus-poor sandy soils, while forest patches have soils of a higher humus content with brown forest soils below, buried by the sand (Bodrogközy 1957, 1982).

The vegetation of the nature reserve consists of a mosaic of forest stands (*Populus alba* variant of the *Populo canescenti-Quercetum roboris* association) and xeric grasslands (mainly *Festucetum vaginatae* association) (Bodrogközy 1957) (Fig. 2). The present pattern is similar to the last natu-
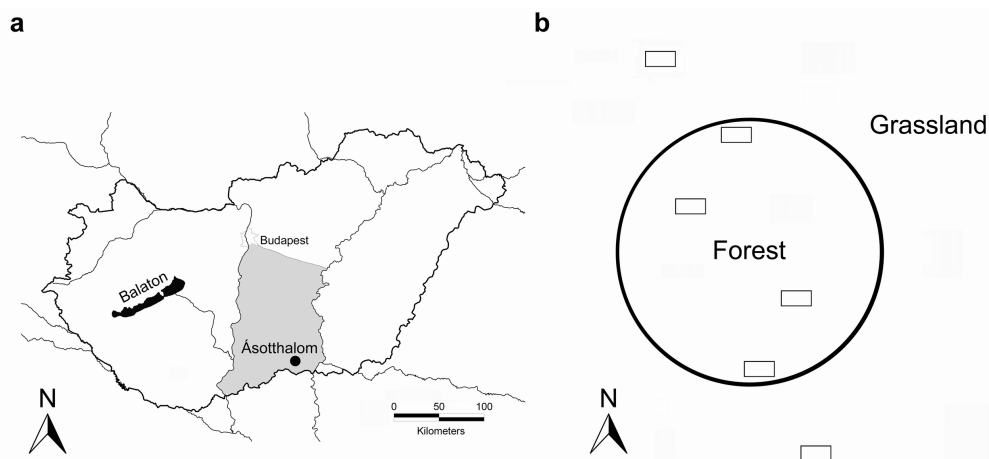

Figure 1. a) The location of the study site in Hungary. Grey shaded area shows the Danube-Tisza Interfluve. **b)** Schematic representation of the study plots concerning one forest patch.

Figure 2. Mosaic vegetation of the study area consisting of forest patches and xeric grasslands.

ral pattern of the region before intensive human impact (Soó 1929, Bodrogközy 1956, Niklfeld 1964, Zólyomi 2007). According to landscape historical researches, poplar trees have dominated the forest patches in the southern part of the Danube-Tisza Interfluve for at least 200 years (Biró et al. 2008). It is assumed that these poplar forests derived from oak forests (Bodrogközy 1957, Soó 1964), probably because gradually drying conditions facilitated clonally spreading poplar trees (Bodrogközy 1982). Sandy forest is not considered the terminal stage of succession (Fekete 1992), thus grasslands do not turn into forests under the present climatic conditions. Forests depend on fossil brown forest soils, buried about 1 m beneath the surface (soils of the ancient oak forests). Forest development, however, is prevented where no such forest soil is available (Bodrogközy 1956, 1982, Fekete 1992). Strong abiotic constraints such as soil properties, coupled with biotic feedbacks, often result in stationary boundaries (Peters et al. 2006), which is clearly the case in our study area, where forest edges are stable (Molnár 2003).

In the forest patches, canopy has a cover of 50-60%, dominated by up to 15-16 m tall silver and grey poplar trees (*Populus alba*, *P. × canescens*). In the shrub layer (height of about 1-3 m), *Berberis vulgaris*, *Crataegus monogyna* and *Ligustrum vulgare* are the most typical. The herb layer (5-50 cm) is sparse, supporting some mesic plants (*Cephalanthera rubra*, *Epipactis atrorubens*, *Fallopia convolvulus*, *Geum urbanum*, *Hedera helix*, *Lithospermum officinale*). However, in the openings and on the edges, herb layer cover usually increases.

Grasslands between the forest patches are built up mainly by a fescue steppe. Here, bunches of *Festuca vaginata* (forming the lower herb layer, about 10-20 cm) and *Stipa borysthenica* (forming the upper herb layer, about 50-60 cm) alternate with mosses, lichens and bare soil. Besides, other species typical of sandy grasslands live there, such as *Alkanna tinctoria*, *Dianthus pontederae*, *D. serotinus*, *D. diutinus*, *Fumana procumbens*, *Iris arenaria*, *Onosma arenaria*, *Polygonum arenarium*. In the nature reserve, no grazing and no forestry activities have occurred for more than 100 years (Bodrogközy 1957, Gaskó 2009).

Field works

In the study area, forest patch size varies between a few tens of square meters and 0.5 ha. In this study, only large patches (0.1-0.5 ha) were considered. 12 forest patches were selected, where adventive plants were absent or negligible. 2 m × 1 m permanent plots were established to sample the herb layer of the edges, the grasslands and the forest interiors (Fig. 1b). Study layout was designed so as to enable us to scrutinize differently oriented edges. Six plots belonged to each forest patch: a north-exposed grassland interior, a north-exposed edge, a north-exposed forest interior, a south-exposed forest interior, a south-exposed edge, and a south-exposed grassland interior (Fig. 1b). Cover of all vascular plant species of the herb layer (including tree saplings and low shrubs) was estimated in July 2011 and April 2012. Summer and spring records were combined in the data analyses.

For plot establishment, edge was defined as the zone out of the outmost trunks of trees, below the canopy layer. During preliminary studies, this zone seemed to be a few meters wide, and its vegetation deviated from both the forest and the grassland interiors. It is a closed grassland, with several tall herbaceous dicots (e.g., *Filipendula vulgaris*, *Ranunculus polyanthemos*) and some shrubs (mainly *Crataegus monogyna*). Forest and grassland interior plots were located approximately 10 m away from the edges, where species composition seemed to be typical of habitat interiors.

Data analysis

When analysing communities arranged along gradients, most ordination methods result in a scattergram showing the arch-effect (Podani 2000). In our study, a grassland-edge-forest gradient was supposed. Therefore, Detrended Correspondence Analysis (DCA) (Hill and Gauch 1980) was carried out to examine similarity of the relevés, since DCA is able to eliminate the arch effect. Although the advantages and disadvantages of the DCA are disputed (e.g., Wartenberg et al. 1987, Peet et al. 1988, Jackson and Somers 1991, Podani 2000, Ejrnæs 2000), it has been widely used in ecology recently (e.g., Bátori et al. 2009, Bagchi et al. 2012, Mahdavi et al. 2013) and it makes the interpretation of the results undoubtedly easier. DCA was done by the software Past 2.15 (Hammer et al. 2001), using the presence/absence data of the species.

Species richness and Shannon diversity of the individual plots were determined using Past 2.15 (Hammer et al. 2001). One-way ANOVA and subsequent Tukey's HSD post hoc tests were performed using the stats package of R 2.10.1 (R Development Core Team 2009) to test the differences in species richness and Shannon diversity between the different habitat types and also to test the effect of exposure on the edge habitats. Box-plots were drawn with SPSS 11.5 (SPSS Inc.).

To reveal edge-related species, we identified diagnostic species of all three habitats (forest, edge, grassland). Diagnostic species are species concentrated in certain vegetation units (i.e. species that preferably occur in some vegetation units) (Chytrý et al. 2002). Fidelity measures can be used to identify diagnostic species (Tichý and Chytrý 2006, De Cáceres et al. 2008, Willner et al. 2009). The most appropriate fidelity measures compare observed species frequencies within a vegetation unit with frequencies that would be expected if the species was randomly distributed (Bruelheide 2000, Chytrý et al. 2002). In this study, phi-values were computed as indicators of fidelity (Tichý and Chytrý 2006). Analyses were done using the software JUICE 7.0 (Tichý 2002). Nonsignificant diagnostic species were excluded with Fisher's exact test. In the rare case when a species appeared to be diagnostic for two habitats, only the habitat with higher phi value and stronger significance level was considered.

It is important to note that all diagnostic species were identified on the local scale in this study. However, we also aimed to compare local and regional behaviour of the species of our examination. Therefore, all diagnostic species were categorized according to their regional coenological preference, based on the system of Soó (1980).

We also identified species that were found solely in the edge plots. Since most of them were rare, occurring only in one or two plots (and with low cover values), only those were considered that occurred in at least three plots.

Environmental factors of the three habitats were assessed using species ecological indicator values for temperature, moisture and light intensity. Mean indicator values were calculated from presence/absence data for each relevé. Borhidi's (1995) indicator values are provided in the Appendix. Although the computation of mean values from ecological indicator values may be mathematically problematic (Möller 1992), the procedure seems to perform well in ecological analyses and it also has a theoretical basis (ter Braak and Gremmen 1987, Diekmann 2003, Tölgyesi and Körmöczi 2012). Moreover, indicator values provide a good estimate of the environmental variables of the plots, as confirmed by several detailed measurements (e.g., ter Braak and Gremmen 1987, Diekmann 1995, Barczi et al. 1997, Schaffers and Sýkora 2000, Dzwonko 2001). To test the effect of habitat type and exposure on the mean ecological indicator values, one-way ANOVA and Tukey's HSD post hoc tests were used. Data were visualized with box-plots made in SPSS 11.5 (SPSS Inc.).

Results

Species composition, species richness and Shannon diversity

A total of 124 species were found in the 72 plots. 53 species occurred in the forest interior plots, 86 species in the edge plots and 81 species in the grassland interior plots.

Ordination scattergram of the DCA clearly revealed the grassland-edge-forest gradient in the data (Fig. 3). Along the gradient, edge relevés are situated between the forest and the grassland ones. Among grassland relevés, there is a considerable variation whereas relevés within the forest group and within the edge group are more similar to one another.

Habitat type had a significant effect on species richness (ANOVA: $F_{2,69}=32.462$, p<0.001). According to Tukey's HSD tests, species richness was significantly larger in the edges than either in the forest (p<0.001) or in the grassland (p=0.0309) (Fig. 4a). Habitat type also significantly influenced Shannon-diversity ($F_{2,69}=7.5689$, p=0.0011). Tukey's HSD tests showed that diversity in the edge was significantly (p<0.001) higher than in the forest interior, but only margin-
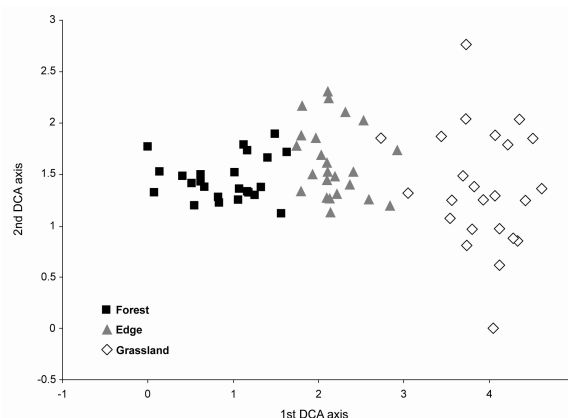

Figure 3. DCA ordination scattergram of the 72 relevés. Eigenvalues of the first two axes were 0.6 and 0.18, respectively.

ally significantly (p=0.058) higher than in the grassland (Fig. 4b).

Edge-related species

Using the fidelity values, 15 forest diagnostic species, 24 edge diagnostic species and 27 grassland diagnostic species could be found (Table 1). Among the edge diagnostic plants, there were four species that were restricted to edges and occurred in at least three plots: *Elymus hispidus*, *E. repens*, *Filipendula vulgaris* and *Ranunculus polyanthemos*.
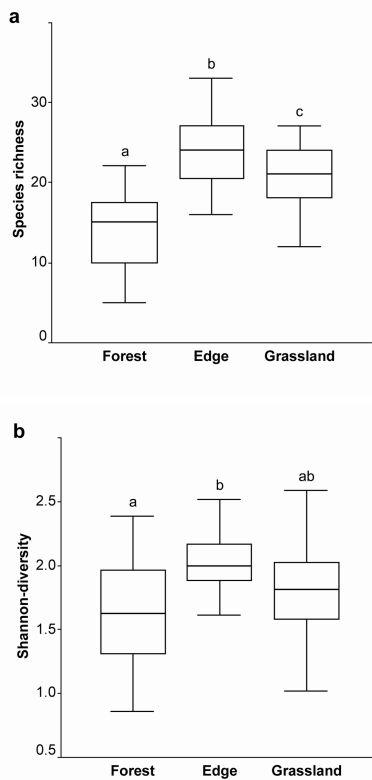

Figure 4. Species richness (**a**) and Shannon-diversity (**b**) of the three habitats. Different letters above the boxes indicate significant differences.
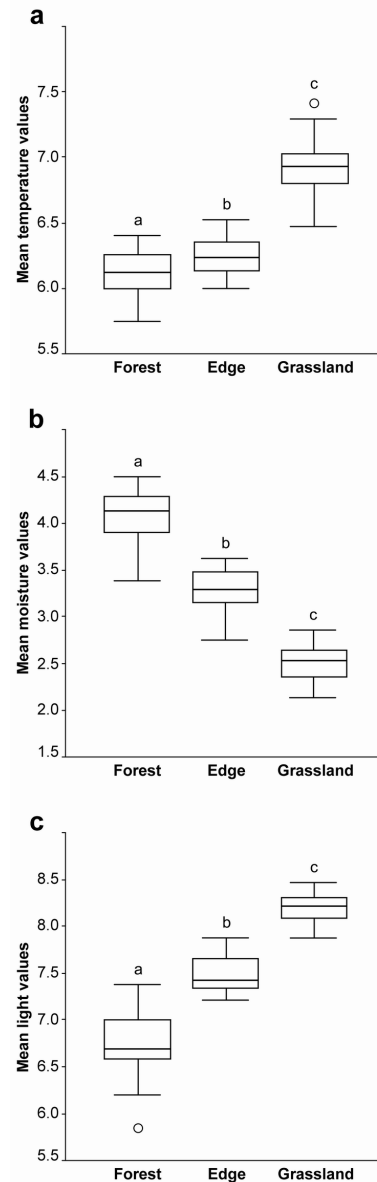

Figure 6. Mean ecological indicator values of the three habitats: (**a**) temperature, (**b**) moisture, (**c**) light. Different letters above the boxes indicate significant differences.
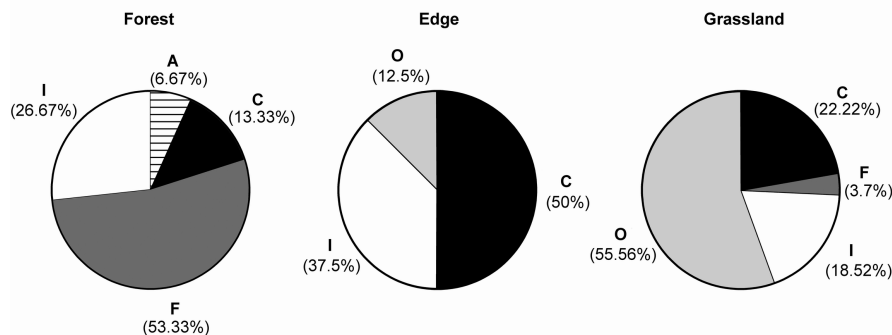

Figure 5. Regional coenological preference of the significant diagnostic species of the three habitats. A: adventive species, C: closed steppe grassland species, F: forest species, I: indifferent species, O: open sandy grassland species.

Table 1. Diagnostic species of the three habitats (forest, edge, grassland). Species that are found exclusively in edges and occur in at least three plots are in bold. coen.: coenological preference, A: adventive species, C: closed steppe grassland species, F: forest species, I: indifferent species, O: open sandy grassland species, *: p<0.05, **: p<0.01, ***: p<0.001.

FOREST DIAGNOSTIC SPECIES	coen.	phi	sign.
Anthriscus cerefolium	I	0.365	**
Berberis vulgaris	F	0.621	***
Celtis occidentalis	A	0.573	***
Crataegus monogyna	F	0.532	***
Cynoglossum officinale	C	0.265	*
Dactylis polygama	F	0.316	*
Fallopia convolvulus	I	0.417	***
Galium aparine	I	0.511	***
Hedera helix	F	0.500	***
Ligustrum vulgare	F	0.511	***
Lithospermum officinale	F	0.265	*
Muscari racemosum	C	0.406	**
Populus x canescens	F	0.437	***
Rhamnus cathartica	F	0.435	***
Stellaria media	I	0.386	**

EDGE DIAGNOSTIC SPECIES	coen.	phi	sign.
Achillea pannonica	C	0.437	***
Asparagus officinalis	C	0.312	**
Bromus sterilis	I	0.388	**
Calamagrostis epigeios	I	0.710	***
Carex liparicarpos	O	0.273	*
Chondrilla juncea	O	0.270	*
Elymus hispidus	C	0.500	***
Elymus repens	I	0.343	*
Eryngium campestre	I	0.471	***
Festuca rupicola	C	0.590	***
Filipendula vulgaris	C	0.295	*
Galium verum	I	0.436	***
Knautia arvensis	I	0.535	***
Medicago falcata	C	0.476	***
Melica transsilvanica	C	0.434	***
Poa angustifolia	I	0.632	***
Ranunculus polyanthemos	C	0.343	*
Seseli annuum	C	0.417	***
Taraxacum officinale	I	0.250	*
Teucrium chamaedrys	C	0.397	**
Thesium ramosum	O	0.270	*
Tragopogon orientalis	I	0.553	***
Verbascum lychnitis	C	0.327	**
Viola rupestris	C	0.389	**

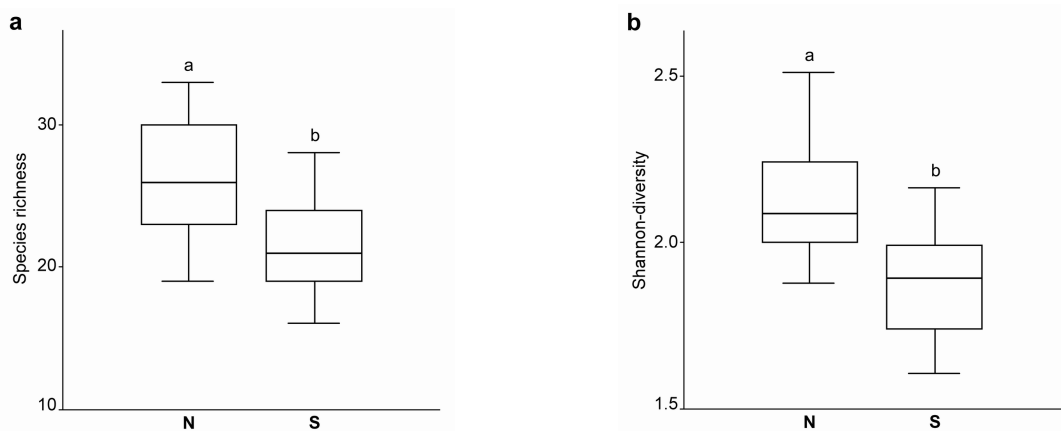| GRASSLAND DIAGNOSTIC SPECIES	coen	phi	sign.
Alyssum montanum	O	0.811	***
Arabis auriculata	C	0.295	*
Arenaria serpyllifolia	I	0.426	***
Artemisia campestris	O	0.295	*
Bassia laniflora	O	0.464	***
Bromus squarrosus	O	0.632	***
Buglossoides arvensis	C	0.343	*
Centaurea arenaria	O	0.553	***
Crepis rhoeadifolia	I	0.426	***
Cynodon dactylon	I	0.389	**
Euphorbia seguierana	O	0.756	***
Festuca pseudovina	C	0.535	***
Festuca vaginata	O	0.816	***
Koeleria glauca	O	0.272	*
Myosotis stricta	I	0.270	*
Onosma arenaria	O	0.343	*
Phleum phleoides	C	0.393	***
Poa bulbosa	I	0.632	***
Polygonum arenarium	O	0.632	***
Populus alba	F	0.370	**
Potentilla arenaria	O	0.439	***
Scabiosa ochroleuca	C	0.454	***
Secale sylvestre	O	0.395	**
Silene otites	O	0.680	***
Stipa borysthenica	O	0.748	***
Thymus pannonicus	C	0.570	***
Viola kitaibeliana	O	0.511	***

Figure 7. Species richness (**a**) and Shannon-diversity (**b**) of the differently oriented edges. N: north-exposed edges, S: south-exposed edges. Different letters above the boxes indicate significant differences.

As it was expected, most forest diagnostic species are regionally regarded as typical of forest communities (Fig. 5). Most grassland diagnostic species are regionally considered open sandy grassland species. More surprisingly, 50% of the edge diagnostic species are typical of closed steppe grasslands regionally, 37.5% are indifferent, and 12.5% are plants of open sandy grasslands, while there are no typical forest species.

Environmental properties of the edges

Habitat type significantly affected mean temperature indicator values ($F_{2,69}=126.53$, $p<0.001$). As shown by the post hoc tests, mean temperature values of the edges were considerably lower than those of the grasslands ($p<0.001$), and higher than those of the forests ($p=0.045$) (Fig. 6.a). Thus, edges were intermediate, but values were much closer to the forest interior. Mean moisture indicator values were also significantly influenced by habitat type ($F_{2,69}=241.09$,

Table 2. Diagnostic species of the north-facing and south-facing edges. *: p<0.05, **: p<0.01, ***: p<0.001.

NORTH-EXPOSED EDGE DIAGNOSTIC SPECIES		
	phi	sign.
Asperula cynanchica	0.447	*
Dactylis polygama	0.447	*
Knautia arvensis	0.430	*
Ranunculus polyanthemos	0.447	*
Seseli annuum	0.753	***
Viola rupestris	0.585	**
SOUTH-EXPOSED EDGE DIAGNOSTIC SPECIES		
Cynodon dactylon	0.530	*

p<0.001); edges differed significantly (p<0.001) from both neighbouring habitat interiors according to the post hoc tests (Fig. 6b). Habitat type had a significant effect on mean light indicator values ($F_{2,69}$=184.87, p<0.001). Mean light indicator values were low in the forest, intermediate in the edge and high in the grassland, differences being highly significant (p<0.001) between the habitats (Fig. 6c).

Differences between south-oriented and north-oriented edges

We could find moderate differences between differently oriented edges. North-facing edges proved to be slightly richer in species ($F_{1,22}$=9.6924, p=0.0051) and more diverse ($F_{1,22}$=14.35, p=0.0010) than south-exposed ones (Fig. 7). North-exposed edges had six diagnostic species, while south-exposed edges possessed one diagnostic species (Table 2). No significant differences were found between differently oriented edges concerning indicator values (mean T: $F_{1,22}$=0.0258, p=0.8739; mean W: $F_{1,22}$=0.0056, p=0.9412; mean L: $F_{1,22}$=0.0212, p=0.8855) (data not shown).

Discussion

Our hypothesis concerning the existence of a distinct edge community, with its own species was verified by the analyses. The DCA ordination indicated that edges in the sandy wooded-steppe mosaic of Hungary deviate from both the forest interior and the grassland (Fig. 3). As the existence of several edge-related species indicates (Table 1), species composition is not simply a mixture of the two neighbouring communities. Instead, edges have their own typical species, not characteristic of any of the habitat interiors. Our results point out that the studied wooded-steppe mosaic has three, and not two integral components, since edges should be recognized as a separate habitat type.

In the sandy wooded-steppe mosaic, higher species richness and Shannon-diversity were found within edges (Fig. 4), which corresponds to the traditional view on forest edge diversity (Odum 1971, Risser 1995). This may have nature conservation implications: in the wooded-steppes of Hungary, conservation efforts must not focus on habitat interiors only, but edges also should be taken into account.

In our study, ecological indicator values suggested that light intensity and temperature of the edges are probably higher than those of the forests, but lower than those of the grasslands. Soil moisture values of edges seemed to be lower than those of the forests and higher than those of the grasslands (Fig. 6). Although more precise measurements would be necessary, it can be assumed that at least some environmental factors are intermediate within edges, compared to forest and grassland interiors. Similarly, the values of certain environmental variables of forest edges have been found intermediate in studies by Magura et al. (2001) and Heithecker and Halpern (2007). According to Ries et al. (2004) transitional values of environmental factors within edges result from ecological flows between habitat patches. However, the results of Chen et al. (1993) and Davies-Colley et al. (2000) indicate that intermediate values of environmental variables within edges may not always be the case (for example, temperature of the edge may be higher than in either neighbouring habitat interior). One possible explanation for this apparent contradiction is that extreme values within edges may be measured under specific circumstances and for short time periods. In contrast, ecological indicator values tend to even out differences in strongly fluctuating variables over time (Zonneveld 1983, Dzwonko 2001). Thus, unlike instrumental measurements, results obtained with indicator values always refer to longer time periods.

Lidicker and Peterson (1999) and Strayer et al. (2003) differentiated between two main types of edges: interactive (or ecotonal) edge and non-interactive (or matrix) edge. An ecological response variable within an interactive edge is larger or smaller than in either of the two neighbouring patch interiors. In contrast, response variable is intermediate in the case of a non-interactive edge (Fig. 8). It seems that in the zonal wooded-steppe of the Hungarian Plain, edges are interactive regarding species composition, species richness and diversity, but they are non-interactive regarding some abiotic parameters. Thus our results emphasize that the very same edge may be interactive and non-interactive at the same time, when different characteristics are considered.

Results of former studies vary enormously concerning the above edge characteristics (species composition, floristic distinctness, edge-related species, diversity and environmental parameters). If generalizations are to be made, natural and man-made edges must be treated separately. In the fine-scale mosaic of the wooded-steppes of the Carpathian Basin, natural forest edges are especially important. In a sandy wooded-steppe of the Great Hungarian Plain, Molnár (1998) found that edges were more diverse than either of the habitat interiors, possessing a distinct species composition with some edge-related species. These results are similar to our findings. However, the extrazonal wooded-steppes of the south-facing mountain slopes (surrounding the Great Hungarian Plain) show entirely different patterns. According to Jakucs (1972) and Erdős et al. (2011), species richness and diversity in mountain forest edges are higher than in the forest interiors, but lower than in the neighbouring grasslands. Furthermore, those edges do not have their own species, but are composed of a mixture of forest interior and grassland interior species. Thus, it seems that lowlands and highlands differ fundamentally as far as edge vegetation is concerned.

If, however, air temperature, evaporation or wind velocity are considered, highland forest edges show transitional values between forests and grasslands (e.g., Jakucs 1959, 1968), which is similar to our findings in Ásotthalom.

The lack of a distinct edge community in the case of the mountain forests is probably due to the soil characteristics, because the shallow and poor soil among the rocks and stones prevents the establishment of additional species (cf. Jakucs et al. 1970). As for the different edge diversity patterns, the diversity of the adjacent grassland and forest should also be taken into account. In the case of the lowland wooded-steppe, low-diversity grasslands and low-diversity forests meet at the edges. In contrast, in the case of highland extrazonal wooded-steppes, extremely high-diversity grasslands form contacts with low-diversity forests. Therefore, the diversity of the edges (lacking edge-related species) cannot exceed the diversity of the neighbouring grassland habitats. Although more case studies are needed to reach a firm conclusion, the above tentative consideration may serve as a useful starting point for further studies.

It is probable that man-made edges are much more variable. As Jakucs (1968, 1972) pointed out, man-made edges often have highly different species composition and structure, even within the same area, as a consequence of their different origin, age and maintenance. As a result, even apparently similar edges can show different edge responses (e.g., Mészáros 1990, Łuczaj and Sadowska 1997, Orczewska and Glista 2005, Dąbrowska-Prot and Wasiłowska 2010).

Most species that proved to be edge-related locally, are typical of closed steppe grasslands regionally (Fig. 5). The probable explanation for this phenomenon is that steppe species do not tolerate very hot and dry conditions, and cannot live in the open sandy grasslands. On the other hand, they cannot grow under the shade of the canopy either. Thus, their occurrence is limited to forest edges, where environmental factors resemble those of the moderately dry steppe grasslands. It was recognized in previous studies that some species typical of edges at a given site may well be found in habitat interiors elsewhere (Lloyd et al. 2000, Erdős et al. 2011), which was clearly the case in the present study. It is doubtful
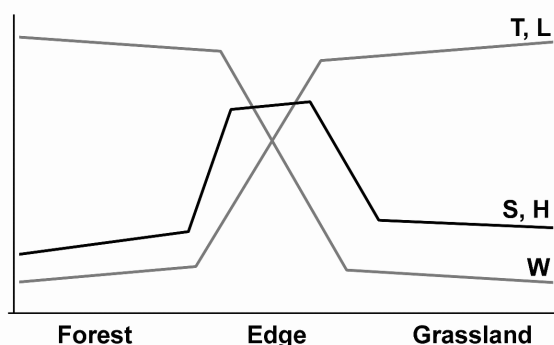
whether edge species in the strict sense (i.e. related exclusively to edges throughout their distribution) exist at all. According to Jakucs (1972), plants that are usually considered edge-species, are confined to edges only in certain areas and sometimes as a result of human activity. It is highly probable that most edge-related species tend to be restricted to edges only locally; therefore, we suggest that they should be referred to as local edge species.

Forest interiors had relatively low species numbers (Fig. 4a) and few diagnostic species (Table 1). This is in accordance with previous studies, which found that the number of typical forest species gradually decreases towards the southeastern part of the Danube-Tisza Interfluve (Fekete et al. 1999, 2010, Biró et al. 2008). The most probable explanation for this is that temperature increases and precipitation decreases from Northwest to the Southeast (Borhidi 1993, Kun 2001), resulting in a more open canopy layer in the forest patches (Fekete et al. 1999, Kovács-Láng et al. 2000, Biró et al. 2008). As a consequence, species-pool of the forests lacks several forest species that are common in the northwestern, less arid part of the Danube-Tisza Interfluve. Another reason can be that, unlike the northwestern parts, the southeastern parts of the Danube-Tisza Interfluve are far away from hilly and mountainous areas, which could serve as potential sources of forest species (Fekete et al. 1999, 2010). Nevertheless, it should be noted that forest interiors do harbour species that are important from a nature conservation perspective (e.g., *Botrychium lunaria*).

In this study, in conformity with our hypotheses, species richness, Shannon diversity and the number of edge-related species were lower in south-oriented than in north-oriented edges (Fig. 7., Table 2.). These results correspond to former studies (e.g., Brothers and Spingarn 1992, Fraver 1994, Burton 2002). Moreover, edge width also seems to vary among edges facing various directions (Fraver 1994). Different edge widths are possible in the wooded-steppe of Hungary, but our study did not measure this property.

On the northern hemisphere, south-facing edges receive more solar radiation, and are usually drier and warmer than north-facing ones (e.g., Chen et al. 1993, Heithecker and Halpern 2007). Surprisingly, no significant differences were revealed between mean ecological indicator values of differently exposed edges in the present study. However, we have to emphasize that the use of relative ecological indicator values is limited when habitats with subtle environmental differences are compared. If differences between the habitats are too small, random fluctuations in species' occurrences have a larger impact on the average indicator values than habitat differences (Diekmann 2003). Potential microclimatic differences between north-facing and south-facing edges may be shown by detailed instrumental measurements.

Figure 8. Interactive (black) and non-interactive (grey) edge-responses along an idealized forest-edge-grassland gradient in the wooded-steppe of the Great Hungarian Plain. T: temperature, L: light, S: species richness, H: Shannon-diversity, W: moisture.

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Electronic Appendix

Relative ecological indicator values of Borhidi (1995) for the species found in the study plots.

The file may be downloaded from the web site of the publisher at www.akademiai.com.