



Original Research Article

Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications

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ABSTRACT

Eurasian forest-steppes are among the most complex ecosystems in the northern temperate zone. Alternating forest and grassland patches form a mosaic-like landscape, stretching in a stripe from eastern Europe almost to the Pacific coast. Although the edges (contact zones between woody and herbaceous vegetation) may play an important ecological role, their study has been neglected in the forest-steppes. In this study, we aimed to perform a comprehensive analysis on the components of a sandy forest-steppe in the Pannonian ecoregion (Hungary), with special regard to the edges. 2 m × 1 m coenological relevés were made in forest interiors, in edges and in grassland interiors. We carried out microclimate measurements in each habitat type. Compositional and structural characteristics of the forests, edges and grasslands were compared, including species number, Shannon diversity, summarized cover, life-form and geoelement spectra. Diagnostic species for each habitat type were identified, and the role of the habitats in harbouring protected and endemic species was also assessed. Based on the frequencies and cover values of tree seedlings and saplings in the three habitat types, we formulated tentative assumptions on vegetation dynamics. We found that edges possessed their own distinct species composition, having a considerably higher species number, Shannon diversity and vegetation cover than habitat interiors. Edges hosted relatively large numbers of edge-related species, and proved to be highly different from habitat interiors with regard to life-form and geoelement spectra. It seemed that the spatial interaction of two neighbouring communities resulted in the emergence of a third, unique community, the edge. The microclimate of the forests and the grasslands differed strikingly, whereas that of the edges fell between them. Except *Populus alba*, trees had very few seedlings and no saplings, which may have serious consequences if the current warming and drying trend continues. We conclude that in the study area, intermediate microclimate of the edges supports a community that is not intermediate compositionally and structurally: the edge should be recognized as a distinct community, although strongly connected to the neighbouring communities. As a consequence, forest-steppes have three integral components: forest, grassland and edge. Our results emphasize the conservation importance of all components. The conservation value of the sandy grasslands has long been recognized, but the contribution of edges and forest patches to species and habitat diversity should not be neglected either. Conservation activities should focus on maintaining the complexity of the forest-steppe ecosystem, with all of its integral components.

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1. Introduction

Complex forest-grassland ecosystems are currently in the focus of ecological interest (e.g. House et al., 2003; Gillson, 2004; Dohn

et al., 2013). On the northern hemisphere, the forest-steppe zone represents such a complex system. This is a tension zone between the closed forests and the steppes, stretching from eastern Europe through Asia almost to the Pacific coast (Borhidi, 2002; Walter and Breckle, 2002; Magyari et al., 2010). In most of this zone, large forests alternate with extensive grasslands (Wendelberger, 1989; Zólyomi and Fekete, 1994; Borhidi, 2002). The Pannonian ecoregion (including the whole area of Hungary) hosts the westernmost forest-steppes (Zólyomi, 1964; Fekete et al., 2002). Here, both forest and grassland patches are considerably smaller than east of the Pannonian ecoregion, resulting in a fine-scale

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micromosaic (Wendelberger, 1989; Zólyomi and Fekete, 1994). Forest patches are usually non-confluent and have a diameter of 10–100 m. This pattern results in a structurally, compositionally and microclimatically extremely complex ecosystem. In addition, the proportion of edges compared to habitat interiors is significantly greater than in other forest-steppe regions, thus their ecological role may be of considerable importance.

Edges (also called ecotones, boundaries or transitional zones) are currently regarded as important components of landscapes and ecosystems (Cadenasso et al., 2003b; Ries et al., 2004; Yarrow and Marín, 2007; Hufkens et al., 2009; Erdős et al., 2011b). Separating two neighbouring communities, edges control the flows of organisms, materials, energy and information (Wiens, 1992), they affect population interactions (Fagan et al., 1999), serve as habitats (Kolasa and Zalewski, 1995) and may have a role in evolutionary processes (Kevey and Borhidi, 1998). Edges are important study objects for community ecology, landscape ecology and nature conservation (Yarrow and Marín, 2007).

There have been many in-depth studies on the coenology of forest-steppes both in Hungary and in other countries (e.g. Máthé, 1933; Zólyomi, 1957; Niklfeld, 1964; Szodfridt, 1969; Tzonev et al., 2006; Butorac et al., 2008; Semenishchenkov, 2012a,b). However, the overwhelming majority of these studies focused either on the forest or on the grassland component separately. More specifically, analysis of forest edges, the contact zones between woody and herbaceous vegetations, has largely been neglected. The importance of edge-studies has been stressed by Wendelberger (1973, 1986), but there seems to be a lack of detailed field studies. Although some researches have already been conducted on the forest edges of mountain areas in the Pannonian ecoregion (e.g. on vegetation: Jakucs, 1972; Erdős et al., 2011a; on microclimate: Jakucs, 1959, 1968; on soil characteristics: Jakucs et al., 1970), results from highlands should not automatically be applied to lowlands.

It is disputed whether forest edges form separate communities with their distinct species composition or they should be put under the umbrella of the forest stand (for a detailed discussion, see Papp, 2007). Several studies have shown that edges bear a resemblance to forest interiors (e.g. Jakucs, 1972; Mészáros, 1990; Orczewska and Glista, 2005; Santos and Santos, 2008), though this pattern is not general: for example, Dierschke (1974) and Erdős et al. (2011a) found that edges were more similar to the neighbouring grasslands than to forest interiors. According to Murcia (1995), the species composition of forest edges is determined primarily by their physiognomy. Thus, it can be hypothesized that edges possessing a dense shrub layer are more similar to the adjacent forest interiors due to the microclimatic effects of shading. In contrast, where no such shrubby fringe exists, edges are expected to resemble to the grasslands.

The problem of the distinctness of edge composition is related to the existence of edge-species. It was assumed by several authors that edges support species from both neighbouring communities as well as their own species, which would result in an increased diversity (e.g. Leopold, 1933; Odum, 1971; Pianka, 1983). However, the situation is probably more complicated, as emphasized by Hansen et al. (1988). Since field studies show inconsistent results, more in-depth studies are needed in this field (Kark and van Rensburg, 2006; Erdős et al., 2011b).

Edges can also be defined structurally, as their physiognomy may differ both from forests and grasslands (Papp, 2007). Several characteristics, including biomass, life-form spectra and geo-element spectra of the constituent plant species may differ between edges and habitat interiors (cf. Ries et al., 2004).

Biotic responses at edges may be explained by altered abiotic conditions (Ries et al., 2004; Kupfer et al., 2006). However, causal relationships between abiotic and biotic edge-effects should be

tested by precise measurements and the most important background factors should be identified (Murcia, 1995; Ries et al., 2004). In the case of sandy forest-steppes Bodrogekőzy (1956, 1957) found that soil factors (primarily the humus content of soil layers buried below the sand) determine where trees can fully develop. However, the importance of microclimate has not yet been investigated in our study area. Although it can be assumed that edge microclimate is influenced by the neighbouring forest stand, the magnitude of this effect is not known.

The dynamics of complex forest-grassland ecosystems belongs to the most interesting issues in ecology, both from a theoretical and a practical perspective (cf. House et al., 2003). In several regions, the proportion of woody vs. herbaceous components is undergoing major changes currently. Most usually, forests and shrubs are spreading at the expense of grasslands (e.g. Archer et al., 1988; Molelele and Perkins, 1998; van Auken, 2000; Roques et al., 2001). Interactive effects of fire regime and grazing pressure are considered the main driving factors, but global changes may also play an important role in dynamic processes (e.g. Archer et al., 1995; Silva et al., 2008). Similar processes have been observed in the Pannonian ecoregion, although underlying mechanisms are not fully understood yet (Somodi et al., 2004; Centeri et al., 2009; Erdős et al., 2014).

Forest edges are believed to play a key role in landscape dynamics (Risser, 1995; Peters et al., 2006). A basic distinction can be made between stable and dynamic edges (cf. Strayer et al., 2003; Peters et al., 2006). If edges are stable, the size of the vegetation patches also remains stable. In contrast, moving edges make vegetation patches expand or contract. Clearly, long-term studies are the best choice to scrutinize such processes. Nevertheless, estimating tree seedling and sapling frequency and cover may also provide useful information on dynamic processes that can be applied as a starting point for further analyses (cf. Montaña et al., 1990; de Casenave et al., 1995; Benitez-Malvido, 1998; Hennenberg et al., 2005b). If tree canopies and shrubs extend above the edge, they probably alter abiotic parameters, which is likely to favour tree seedling establishment and survival. Growing trees, in turn, further modify their environments, enabling the existence of more and more forest species. These community-induced changes can result in an advancing edge, and consequently, forest expansion (Weltzin and McPherson, 1999; Peters et al., 2006; Silva et al., 2013b).

In this study, our aim was to give a comprehensive analysis of the herb layer of the edges in a lowland forest-steppe landscape. We tested if edges form a distinct community or they belong to one of the neighbouring habitat interiors. We identified edge-species, and scrutinized some vegetation characteristics of the edges (species number, diversity, life-form and geo-element spectra) as compared to the forest and grassland interiors. We made an attempt to assess the number of protected and endemic species occurring in each individual habitat. Moreover, we carried out microclimate measurements (air temperature and air humidity) in all three habitats, and identified their importance in shaping the vegetation of the study area. Finally, we investigated the role of the edge and interior habitats in vegetation dynamics, by analysing the frequency and abundance of tree seedlings and saplings.

As a starting point, it was reasonable to assume that forests and grasslands form separate, distinct communities. Moreover, since forest canopy and shrub layer extend above the edges in our study area, we hypothesized that trees have a fundamental effect on the microclimatic conditions not only within the forest patch, but also in the edge. As a result, we expected that species composition, diversity, vegetation cover and other structural characteristics of the herb layer of the edges would be similar to those of the forest interiors. According to our hypothesis, edges would not form a distinct community and would possess rather few diagnostic

species. We also expected that seedlings and saplings of the native tree species would be represented by many individuals and high cover values within edges, possibly contributing to forest expansion.

2. Materials and methods

2.1. Study area

We selected two study sites (site A: N 46°17', E 19°35' and site B: N 46°12', E 19°47') in southern Hungary, between River Danube and River Tisza (Fig. 1), where stabilized sand dunes occupy large areas (Várallyay, 1993). The distance between the two sites is about 17 km. The two sites are remarkably similar, with the same plant associations, but sand dunes are higher in site A (~5 m) than in site B (<2 m). The mean annual temperature is 10.6 °C and the mean annual precipitation is 580 mm (Ambrózy and Kozma, 1990). Grasslands have humus-poor sandy soils, whereas forest patches grow on sandy soils with a somewhat higher humus content (Bodrogközy, 1957, 1982).

Site A is a protected area since 2004. Site B has been protected since 1908, and no grazing or forestry activities have occurred there during the last hundred years (Gaskó, 2009). Both sites have a vegetation that seems almost natural, both in terms of structure and composition. This is further emphasized by a remarkably high number of protected plants.

The vegetation of the study areas is a remainder of the originally extensive forest-steppes of the Pannonian ecoregion. In the forest patches, the canopy has a cover of 50–60%, dominated by up to 15–16 m tall silver poplar trees (*Populus alba*) and some *Quercus* species (*Quercus rubur*, *Qu. cerris* and *Qu. pubescens*). In the shrub layer, *Berberis vulgaris*, *Crataegus monogyna* and *Ligustrum vulgare* are the most abundant. The herb layer is codominated by xeric (e.g. *Carex liparicarpos*, *Teucrium chamaedrys*) and mesic plants (e.g. *Anthriscus cerefolium*, *Hedera helix*, *Stellaria media*). Usually, about 80% is covered by litter and bare sand.

Grasslands are dominated by *Festuca vaginata* and *Stipa borysthenica* but *Bassia laniflora*, *Centaurea arenaria*, *Colchicum arenarium*, *Euphorbia seguierana* and *Fumana procumbens* are also common. The cryptogamous layer, consisting of various mosses and lichens, also has a considerable cover. Bare sand surfaces cover 50–70%.

2.2. Field work

In both sites, ten natural forest patches were selected. During forest patch selection, the following criteria were used. First, those forest patches were selected that were surrounded with near-

natural grasslands in every direction, based on aerial photos and subsequent field surveys. Of these patches, after preliminary field surveys, the most natural ones were chosen for our analyses (where human disturbance and invasive species were absent or negligible). To exclude the effect of different exposures, only north-facing edges were analyzed in this study. North-facing edges were supposed to be more strongly influenced by the shading effect of the forest patch. Concerning each forest patch, three 2 m × 1 m coenological relevés were made (forest interior, north-facing edge, grassland interior), resulting in a total of 60 relevés (2 sites × 10 patches × 3 habitats). Forest edges are conceived as three-dimensional structures, but their width dimension is usually small (Cadenasso et al., 2003a; Erdős et al., 2011b). For the present study, edge was defined as the zone out of the outmost tree trunks, but under the canopy. Earlier studies in the region revealed that the zone between the outmost tree trunks and the open area, shaded by tree canopies, should be considered the transitional zone (Jakucs, 1972; Mészáros, 1990). Preliminary studies showed that edges are rather narrow, therefore, the elongated plot shape seemed to be a reasonable choice, not extending into habitat interiors. The midpoints of the plots were placed randomly within each habitat. Cover of all vascular plant species of the field layer (including tree saplings and low shrubs) was estimated in April and July. Spring and summer cover values were combined during data analysis. Species names follow the nomenclature of Simon (2000).

For an additional analysis, we made extensive field surveys to compile the complete list of protected and/or endemic species of the three different habitats for the whole study area.

2.3. Microclimate measurements

For microclimate measurements, nine plots were selected (three in different forest patches, three in the northern edge of these forest patches and three in the adjacent grasslands). We measured temperature (°C) and air humidity (%) 25 cm above the ground surface for 24 h. 50 IRIS (XM2110CA) wireless sensors from Crossbow® were applied, each of which were equipped with an MTS400 (SN21140CA) weather sensor board. Signals from the sensors were measured once every minute and from these data the daily minimum and maximum air temperature (DMinAT, DMaxAT) and air humidity values (DMinAH, DMaxAH), the mean daily air temperature (MDAT) and air humidity values (MDAH), the mean daytime air temperature (MDtAT) and air humidity values (MDtAH) and the mean nighttime air temperature (MNtAT) and air humidity values (MNtAH) were calculated. 'Daytime' is defined as the time period between 7 a.m. and 7 p.m., while 'nighttime' as the period between 7 p.m. and 7 a.m. All microclimate measurements were carried out after a dry period, under mostly clear weather conditions on August 2 and 3, 2012.

2.4. Data analysis

The number of protected and/or endemic species was displayed in a Venn diagram (created by the 3-way Venn Diagram Generator of Whitehead BaRC).

To reveal the similarity of the relevés within each habitat type, as well as to compare the three different habitats, PCoA ordination was performed on the raw percentage cover values, using the programme package SYN-TAX 2000 (Podani, 2001). As dissimilarity function, Canberra metric was applied.

Diagnostic species were identified by calculating phi-coefficients as indicators of fidelity (Tichý and Chytrý, 2006). Non-significant diagnostic species were excluded with Fisher's exact test. Analysis was done using the JUICE 7.0 software (Tichý, 2002). Functional types and life-form categories of all diagnostic species were given, according to Simon (1988) and Horváth et al. (1995),

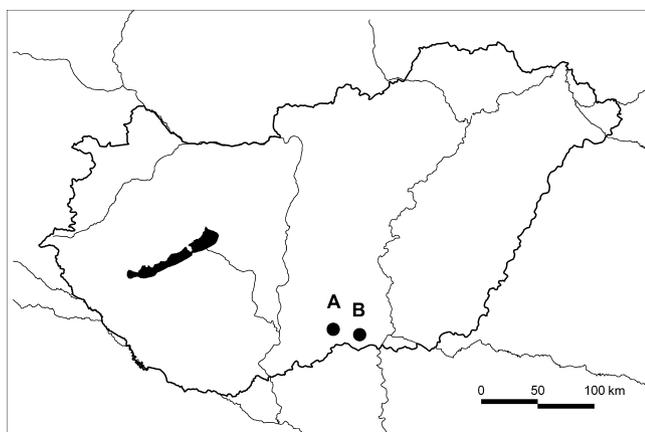


Fig. 1. Location of the study sites in Hungary.

respectively. Simon's (1988) functional types are based on how species tolerate disturbance and competition pressure, and indicate their role in plant communities.

To have an idea about the spatial distribution of the most abundant species, we averaged the cover values, and displayed them according to their spatial position. As an additional analysis, a Venn diagram was generated, based on the occurrence of all species encountered during field works.

Generalized linear models were built to reveal whether habitat type (forest, edge, and grassland) had a significant influence on species number, on Shannon diversity and on the summarized vegetation cover. Habitat type was treated as a fixed effect and locality (sites A and B) as a random effect. Tukey's pairwise comparisons were applied as post hoc tests. For these analyses, SPSS 11.5 was used (SPSS Inc.). Species number and Shannon diversity was calculated with Past 2.17.b (Hammer et al., 2001).

Every recorded species was classified into life-form and geoleme categories according to the FLÓRA Database (Horváth et al., 1995). Spectra were calculated from species cover data for each habitat type.

Variation of species presence/absence data was related to temperature and humidity measurements by distance-based redundancy analysis (db-RDA), applying the complement of Sorensen index as a distance measure. The following factors were used as explanatory variables: MDAT, MDtAT, MNtAT, MDAH, MDtAH and MNtAH. The gross effect of each climatic variable was calculated by constructing a db-RDA model with the tested variable as the only predictor and the compositional data as the dependent variables ('one-predictor model'). Effect strength of each climatic variable was quantified by the percentage explained variance and F value of the respective db-RDA model, and their significance was assessed by a permutation test. After this, the most effective temperature and the most effective humidity variables were selected, based on the lowest p and the highest F values. With these two as background variables, a new db-RDA was performed ('two-predictor model') in order to assess the cumulative effect of the best climatic variables. There were high colinearities among different temperature variables (i.e. MDAT, MDtAT, and MNtAT) and among different humidity variables (i.e. MDAH, MDtAH, and MNtAH), thus the less effective variables were not involved in the model. The 'two-predictor model' was visualized on a biplot diagram. Distance-based redundancy analysis was performed using the Vegan R package (Oksanen et al., 2009; R Development Core Team, 2009).

To assess the role of the individual habitats in vegetation dynamics, we paid special attention to the seedlings (<5 cm) and saplings (5–50 cm) of the native tree species. We summarized their cover values over all plots within the habitats, and calculated their frequencies.

3. Results

In the 60 plots, a total of 130 species was recorded. The most abundant species of the forest interiors were *Bromus sterilis*, *Carex liparicarpus* and *Fallopia convolvulus*, those of the edges were *Crataegus monogyna*, *Festuca rupicola*, *Poa angustifolia* and *Teucrium chamaedrys*, while grasslands were dominated by *Festuca vaginata*, *F. pseudovina*, *Stipa borysthena* and *Thymus pannonicus*.

During the field studies, 19 protected and/or endemic plant species were found. The most valuable habitat from this point of view is the grassland, while the forest patches harbour relatively few of these species (Fig. 2).

Results of the PCoA ordination showed that the relevés formed three relatively distinct groups in the scattergram, according to the grassland, forest and edge habitats (Fig. 3). Forest plots were similar to one another, while grassland plots were somewhat more

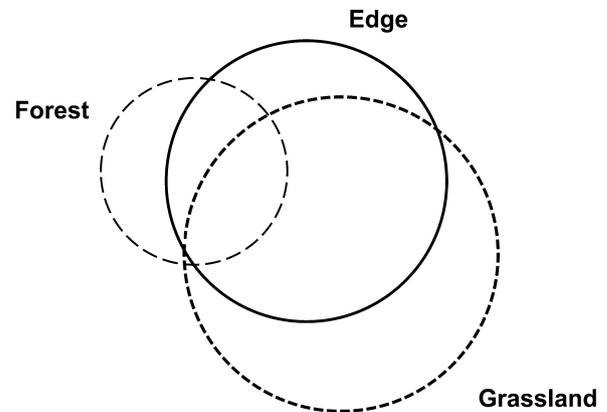


Fig. 2. Proportional Venn diagram of all protected and/or endemic plant species of the study area, according to their habitat. Areas in the diagram are proportional to the number of species they represent.

scattered. Edge relevés formed the least compact group, indicating a high variation of the edge habitat.

Significant ($p < 0.001$) diagnostic species are listed in Table 1. The edge habitat had 13 diagnostic species. Forest interiors hosted 6, grassland interiors 10 diagnostic species. Concerning functional types, edge diagnostic species were competitors, accompanying species or disturbance tolerants. Regarding life-form categories, most of them were hemicryptophytes (among them, some grasses). In both respects, edges were more similar to grasslands than to forests.

Based on their spatial distributions, the most abundant species could be ordered into two groups (Fig. 4a). Some species reach their maxima in the grassland, occurring towards the edge and forest interior with decreasing abundance. Other species have the highest cover values within the edge, and are represented in habitat interiors mostly with smaller cover values. (The species that have maximum cover values within the forest interior are not displayed, due to their low cover values.) Fig. 4b shows that many species are restricted to one habitat type. Nevertheless, the three habitats under study are strongly inter-connected: the overlapping areas are considerable, indicating that several species occur in two or three habitats.

According to the generalized linear model, habitat type significantly influenced species number ($F = 23.602$, $p < 0.001$). Tukey's post hoc comparisons showed that the species number of the edge was significantly higher than that of the habitat interiors (edge vs. grassland: $p < 0.001$; edge vs. forest: $p < 0.001$). Species number of the forest and the grassland did not differ significantly ($p = 0.351$) (Fig. 5a).

Habitat type also had a significant effect on the Shannon-diversity ($F = 11.114$, $p < 0.001$). Again, the edge proved to be more diverse than habitat interiors (edge vs. grassland: $p < 0.001$, edge vs. forest: $p = 0.001$). The diversity of the forest and that of the grassland did not differ significantly ($p = 0.913$) (Fig. 5b). Between-site differences were not significant regarding either species number ($F = 3.210$, $p = 0.079$) or Shannon diversity ($F = 0.189$, $p = 0.666$).

Finally, habitat type significantly affected summarized vegetation cover, as shown by the generalized linear model ($F = 82.523$, $p < 0.001$). Edges had higher cover values than either the forest interiors ($p < 0.001$) or the grasslands ($p = 0.001$). The difference was significant between the forest and the grassland as well ($p < 0.001$) (Fig. 6). In the case of the cover values, between-site differences proved to be significant ($F = 15.028$, $p < 0.001$).

Regarding life-form categories, the three different habitats had considerably different structures (Table 2). Annuals and geophytes

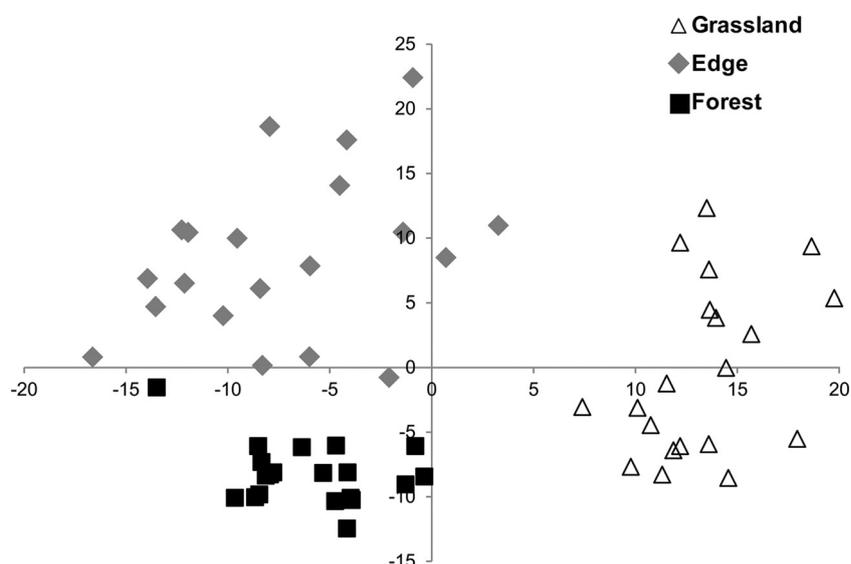


Fig. 3. PCoA ordination scattergram of the 60 relevés. Percentage variances explained by the first and second axes are 21.31% and 15.31%, respectively.

had their maxima in the forest patches, but trees and shrubs were also the most abundant here. Small shrubs and biennials reached the highest proportion within edges, while hemicryptophytes and dwarf shrubs had the highest proportion in grasslands.

Concerning geoelements, all habitat types were dominated mostly by continental and European species (Table 3). In general,

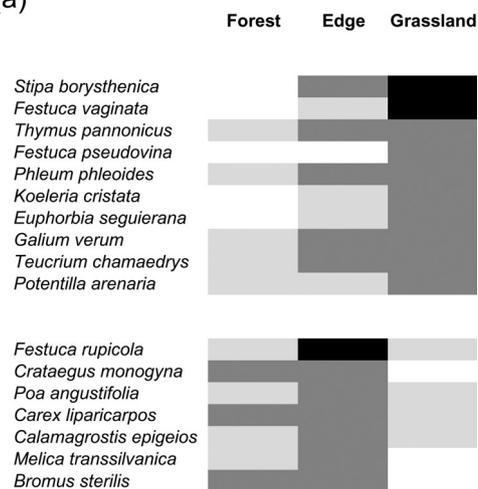
grasslands seemed to have a more continental character. It is important to note that forests harboured the most adventives, and grasslands provided habitat for a surprisingly high amount of endemics.

Table 1

Significant ($p < 0.001$) diagnostic species of the habitat types (i.e. forest, edge and grassland), with fidelity (ϕ) values, functional types (A, accompanying species; C, competitor; DT, disturbance tolerant; NN, non-native; P, pioneer; W, weed) and life-form categories (Ch, dwarf shrubs; H, hemicryptophytes; H (g), hemicryptophyte grasses; M, shrubs; MM, trees; Th, annuals).

	Phi	Functional type	Life-form category
Forest diagnostic species			
<i>Anthriscus cerefolium</i>	0.549	DT	Th
<i>Celtis occidentalis</i>	0.420	NN	MM
<i>Crataegus monogyna</i>	0.384	A	M
<i>Fallopia convolvulus</i>	0.625	W	Th
<i>Galium aparine</i>	0.739	W	Th
<i>Rhamnus cathartica</i>	0.514	A	M
Edge diagnostic species			
<i>Achillea pannonica</i>	0.476	A	H
<i>Calamagrostis epigeios</i>	0.510	DT	H (g)
<i>Crataegus monogyna</i>	0.384	A	M
<i>Festuca rupicola</i>	0.547	C	H (g)
<i>Galium verum</i>	0.472	A	H
<i>Knautia arvensis</i>	0.629	A	H
<i>Medicago falcata</i>	0.560	DT	H
<i>Phleum phleoides</i>	0.433	A	H (g)
<i>Poa angustifolia</i>	0.564	C	H (g)
<i>Seseli annuum</i>	0.579	A	H
<i>Thymus pannonicus</i>	0.360	A	Ch
<i>Veronica prostrata</i>	0.464	DT	Ch
<i>Viola rupestris</i>	0.507	A	H
Grassland diagnostic species			
<i>Alyssum montanum</i>	0.590	A	Ch
<i>Bassia laniflora</i>	0.590	P	Th
<i>Centaurea arenaria</i>	0.667	A	H
<i>Euphorbia seguierana</i>	0.625	A	H
<i>Festuca pseudovina</i>	0.549	C	H (g)
<i>Festuca vaginata</i>	0.750	C	H (g)
<i>Poa bulbosa</i>	0.629	DT	H (g)
<i>Polygonum arenarium</i>	0.585	P	Th
<i>Silene otites</i>	0.543	A	H
<i>Stipa borysthena</i>	0.729	C	H (g)

(a)



(b)

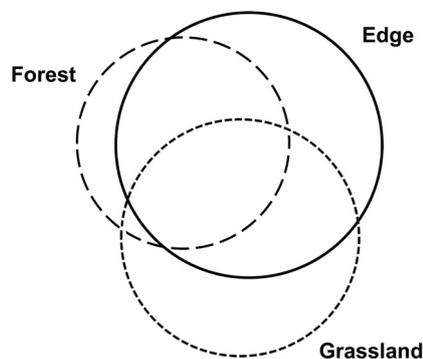


Fig. 4. (a) Spatial distribution of the most abundant species. Average cover values are indicated as follows: black: >10%, dark grey: 1.1–10%, light grey: 0.1–1%, white: 0%. (b) Proportional Venn-diagram of all species encountered in the study area, according to their habitat. Areas in the diagram are proportional to the number of species they represent.

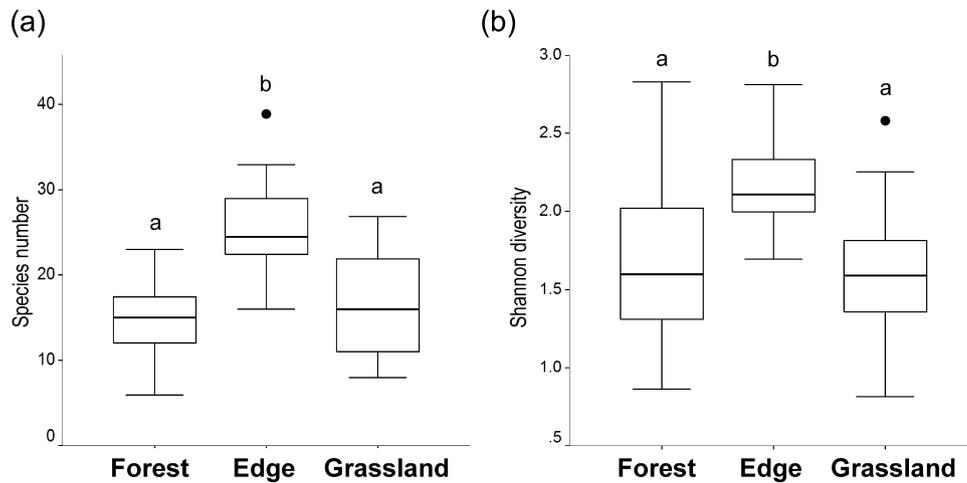


Fig. 5. (a) Species number and (b) Shannon diversity of the forest, edge and grassland habitats. Different letters indicate significant differences.

In the daytime, air temperatures of the grasslands were considerably higher than those of the forests (Fig. 7). Edges were similar to the forests, except for the late afternoon hours, when they were intermediate. During the night, grasslands became cooler than forests, while temperatures of the edges were very close to those of the grasslands. Daily temperature variation was extremely great in the grasslands, where the maximum temperature was close to 45 °C near the soil surface, while the minimum hardly exceeded 15 °C. Within the forest patches, variation was considerably smaller: temperature values ranged between 17 and 37 °C. In the edges, the minimum was a bit over 15 °C, but the maximum value exceeded 40 °C.

Humidity values showed an opposite pattern (Fig. 8). In the daytime, forests were more humid than grasslands and after sunset, the relative humidity of the grasslands began to increase and soon it exceeded the relative humidity of the forests. Edges were mostly intermediate.

The explanatory power of microclimatic variables in the 'one-predictor' db-RDA models is shown in Table 4. Four of the six variables proved to be significant. Of the temperature variables, mean daytime air temperature had the strongest effect. As for the humidity variables, mean daytime air humidity explained the majority of the variation.

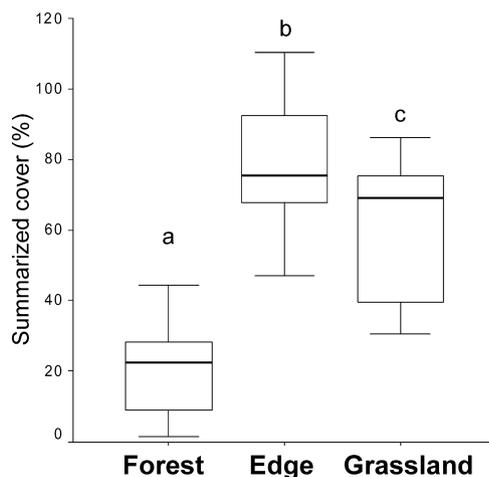


Fig. 6. Summarized cover of the forest, edge and grassland habitats. Different letters indicate significant differences. Lower and higher plants can overlap, thus summarized cover may exceed 100%.

The 'two-predictor' model included mean daytime air temperature and mean daytime air humidity, explaining 50.9% of the total variation ($F = 3.104$, $p = 0.005$) (Fig. 9).

Concerning vegetation dynamics, we found that seedlings and saplings of native trees had relatively low cover values and frequencies in all habitats (Fig. 10). It seemed that different habitats were suitable for the young individuals of the different species. *P. alba* was most abundant and most frequent in the grasslands, and its cover and frequency decreased towards the forest interior (Fig. 10a). In contrast, *Populus × canescens* occurred only in the forest interior habitat. Its frequency was considerable, but its cover was very small (Fig. 10b). Both *Quercus* species were the most frequent and most abundant in the edges. Nevertheless, they were present only in 10–15% of the edge plots, with extremely low cover values (Fig. 10c,d). It should be noted that all *Populus × canescens*, *Qu. cerris* and *Qu. robur* individuals encountered in the herb layer were about 3–5 cm high; the only species having individuals higher than 5 cm was *P. alba*.

4. Discussion

4.1. Vegetation structure and composition

Forest-steppe is the main vegetation type in the Pannonian ecoregion as well as in large areas of eastern temperate Eurasia. Most studies on forest-steppes have presupposed that this ecosystem consists of two components: grassland and forest. In our study, forests, grasslands and edges were also taken into consideration.

Our hypothesis that the edge vegetation would belong to the forest interior, has to be rejected. Edge plots formed a relatively distinct group in the ordination scattergram (Fig. 3), and they

Table 2

Life-form spectra of the different habitats, based on species cover values. Within each row, the maximum is highlighted in grey.

	Forest	Edge	Grassland
Annuals	23.63	3.79	0.91
Biennials	1.98	2.52	1.7
Geophytes	29.87	11.58	3.38
Hemicryptophytes	14.1	59.58	81.35
Dwarf shrubs	3.39	7.18	11.64
Small shrubs	0	0.23	0.02
Shrubs	22.96	14.29	0.08
Trees	4.06	0.84	0.91

Table 3

Spectra of the geoelement categories of the three habitats, based on species cover values. Within each row, the maximum is highlighted in grey.

	Forest	Edge	Grassland
Adv.	4.21	0.41	0.11
Koz.	3.73	1.44	5.35
Con.	37.71	27.42	49.21
Eur.	49.32	63.75	19.80
Atl.	1.36	2.03	0
Med.	3.56	3.97	2.28
End.	0.12	0.99	23.25

Adv., adventives; Koz., Cosmopolitan species; Con., continental species; Eur., European species; Med., Mediterranean species; Atl., Atlantic species; End., endemics.

apparently did not belong either to the grassland or to the forest plots. In addition, several edge-related species were identified (Table 1). Species number, Shannon diversity and vegetation cover of the edges proved to be highly different from both habitat interiors (Figs. 5–6). Life-form and geoelement spectra also support the notion that the edge should be regarded as a separate community (Tables 2–3). However, the strong connections among the habitats should not be under-estimated, as shown by the spatial pattern of the abundant species as well as by the large overlaps of the species pools (Fig. 4). It seems clear that the two adjacent communities (forest and grassland) interact in a way that results in the formation of a third unit, the edge, which should be regarded as a separate and distinct community.

In the Pannonian ecoregion, the existence of a distinct edge community, with its own edge-related species and an increased diversity should by no means be considered a general phenomenon. It seems that a basic distinction should be made between highland and lowland forest-steppes. In the mountainous areas of the Pannonian ecoregion, species composition of the edges of the xeric forests is rather a mixture of the two habitat interiors (i.e. forest and grassland), having only a few own species (Jakucs, 1972; Erdős et al., 2011a). Their species number and diversity are higher than those of the forest interiors, but lower than those of the grasslands and they do not form a separate community type. The situation is different in the case of lowland forest-steppes. Molnár (1998) reported from a lowland forest-steppe that forest edges were species-rich, supporting a relatively large number of edge-related species. These results were highly similar to our present

findings, although there was no overlap between edge-related species found by Molnár (1998) and those identified in our study. This latter fact probably shows that local species pool may determine which species will be concentrated in this habitat type. In the study of Molnár (1998), proportion of specialist species was the lowest in the forest interior and highest in the grassland, while edges were intermediate. This was similar to our results concerning protected and endemic species, most of which are specialists (Fig. 2).

Generally, regarding the vegetation characteristics under study, complex tree-grass ecosystems of South-America and Africa are often quite similar to the lowland Pannonian forest-steppes. For example, Pinder and Rosso (1998) found that in the savannas of the Brazilian Pantanal, forest edges form a distinct community, possessing a high species number and diversity, and a great variety of life-form categories. In addition, the number of typical forest interior species was relatively low, which is also similar to our results. Similar patterns were revealed by de Casenave et al. (1995) in the semi-arid Chaco forest in Argentina, where edges had their own species composition and an increased diversity, although, contrary to our findings, herb layer cover was not significantly different between interiors and edges. Studying a gallery forest edge in southern Brazil, van der Berg and Oliveira-Filho (1999) found that the forest edge had its own characteristic structure, species composition, and several edge-related species. Concerning Africa, Hennenberg et al. (2005a) studied a near-natural forest-grassland mosaic, and they concluded that a relatively well-defined edge community of a considerable width exists.

However, it is important to note that there are some studies with completely different results. For example, according to Santos and Santos (2008), in the xeric scrub of the Brazilian Caatinga, vegetation structure, composition and diversity did not differ significantly between interiors and edges. The probable cause of this phenomenon is that abiotic parameters of the edges and those of the interiors are relatively similar in the case of the Caatinga (cf. Santos and Santos, 2008), whereas they are much more different in the case of the Pannonian forest-steppes.

4.2. Abiotic–biotic relationships

It is widely accepted that altered vegetation characteristics near habitat edges result from modifications of the physical

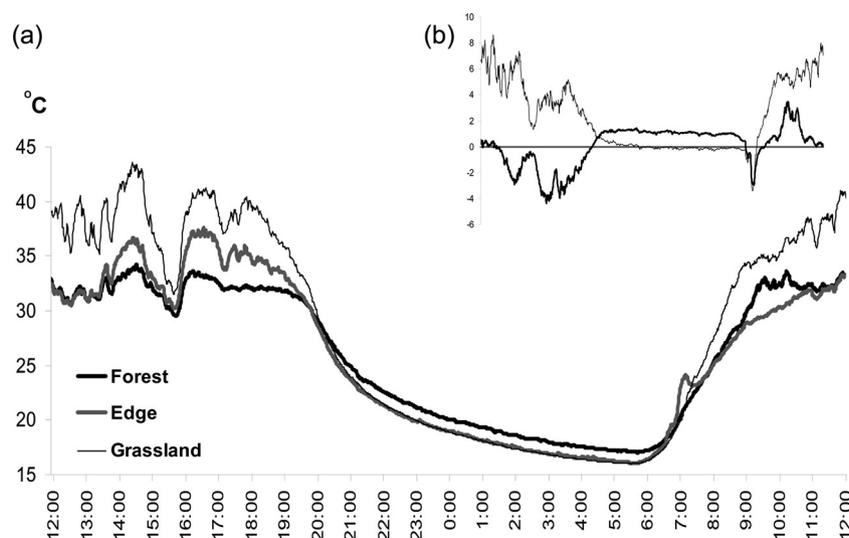


Fig. 7. (a) Temperature values of the habitat types, measured over a 24-h period. Values for every minute are averaged over the three repeats. The drop in the values between 3:00 p.m. and 4:00 p.m. is due to a light shower. (b) Differences of the habitat interiors, as compared with the edge. The horizontal grey line indicates the edge.

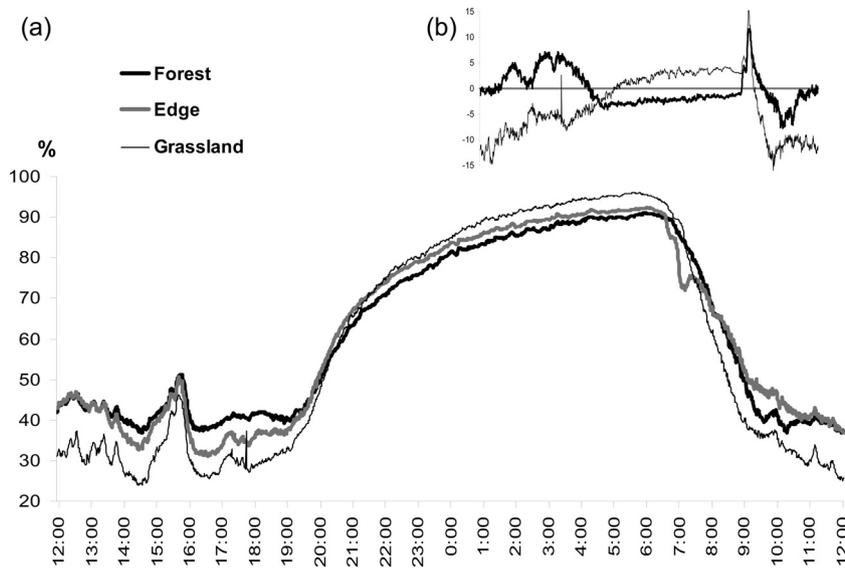


Fig. 8. (a) Humidity values of the habitat types, measured over a 24-h period. Values for every minute are averaged over the three repeats. (b) Differences of the habitat interiors, as compared with the edge. The horizontal grey line indicates the edge.

environment (e.g. microclimate and soil parameters) (Murcia, 1995; Kupfer et al., 2006). In fact, organisms usually map onto abiotic environmental gradients, which has a profound influence on vegetation within edges (Ries et al., 2004).

To test some of the abiotic-biotic connections for the Pannonian lowland forest-steppes, we carried out microclimate measurements. We found that both the air temperature and the air humidity of the edges were greatly influenced by the neighbouring habitat interiors. Instead of being very close to the forest interiors, microclimatic values proved to be rather intermediate (i.e. between the values of grasslands and forest interiors) (Figs. 7 and 8). These results are in good agreement with previous data of Jakucs (1959, 1968, 1972), Jakucs et al. (1970) and Magura et al. (2001). According to their measurements, which were carried out in highland forest edges throughout the Pannonian ecoregion, soil temperature, air temperature, evaporation rate and wind velocity of the edges is transitional. Similarly, transitional abiotic parameters have been found in several other edges between forested and unforested areas in Europe, Africa, North-America and South-America (e.g. Dąbrowska-Prot et al., 1973; Hennenberg et al., 2005b; Heithacker and Halpern, 2007; Hoffmann et al., 2009).

In our analysis, a causal relationship between microclimate and vegetation was sought, using db-RDA. The results of this analysis suggested that microclimate (most importantly the mean daytime air temperature and the mean daytime air humidity) significantly influences species composition, creating three different habitats: forest interior, edge and grassland interior (Fig. 9). Thus, our most important finding is that intermediate microclimate enables the existence of an edge community that is compositionally and

structurally not intermediate, and does not belong to either habitat interior.

Beside air temperature and humidity, several other factors may have a role in determining edge community composition and structure. For example, alterations in soil nutrient supply, soil moisture and solar radiation may be extremely important (Ries et al., 2004).

Detailed soil surveys of Bodrogközy (1956, 1982) showed that, in the case of lowland forest-steppes of the southern part of the Pannonian ecoregion, forest patches always grow on sites where there is a buried layer of brown forest soil with a relatively high humus content. (This layer was buried by sand movements). However, such a buried layer can never be found under the grasslands. This fact seems to play a major role in constraining current forest-grassland dynamics (see Section 4.3). Unfortunately, no soil analyses have been carried out within the forest edges in the study region. Although Wendelberger (1986) suggested that soil features of the edges may be transitional between the forest interiors and grasslands, it is clear that future studies should be made on the edge soils. Such studies will probably enlighten the exact role of forest edges in long-term ecosystem processes.

Table 4
Explanatory power of the microclimatic variables according to the 'one-predictor' db-RDA analyses.

	Var%	F	p
Mean daily air temperature	43.945	5.488	0.007
Mean daytime air temperature	45.387	5.817	0.005
Mean nighttime air temperature	15.686	1.302	0.230
Mean daily air humidity	28.006	2.723	0.045
Mean daytime air humidity	41.583	4.983	0.008
Mean nighttime air humidity	21.793	1.951	0.117

Var%, percentage variance explained.

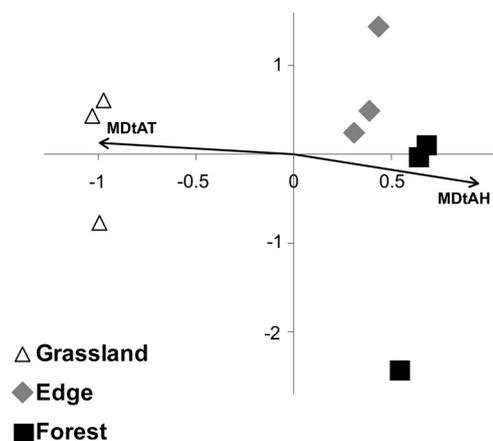


Fig. 9. Biplot of the 'two-predictor' db-RDA analysis. MDtAT, mean daytime air temperature; MDtAH, mean daytime air humidity. Percentage variances explained by the first and second axes are 46.1% and 4.8%, respectively.

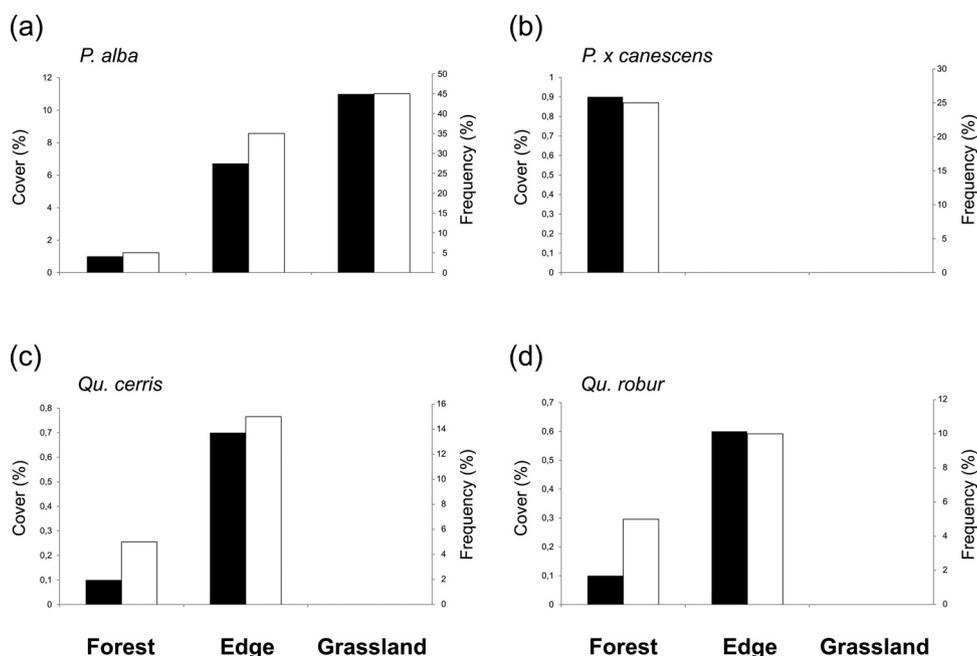


Fig. 10. Summarized cover (black) and frequency (white) values of the native tree species in the forest, edge and grassland habitats. (a) *Populus alba*, (b) *Populus × canescens*, (c) *Quercus cerris*, (d) *Quercus robur*. Note the different scales of the vertical axes.

It was shown that solar radiation within an edge is higher than in the forest interior but lower than in the adjacent open habitat (e.g. Cadenasso et al., 1997; Chen et al., 1999). This proved to be a major factor in shaping plant communities near edges (Honnay et al., 2002; Dignan and Bren, 2003; Watkins et al., 2003). As for the Pannonian forest-steppes, Wendelberger (1986) stated that light conditions are at least partly responsible for creating strongly different grassland, edge and forest communities, although no measurements are available to the best of our knowledge.

The sandy forest-steppes of the Pannonian region grow under extreme habitat conditions. Growing season temperatures and temperature variations are high, while precipitation is low. Water-holding capacity and organic matter content of the sandy soils are extremely low. Under such circumstances, both microclimatic parameters measured in the present study and competition for different resources may be critical for vegetation. The exact role of resources remains to be determined in subsequent studies.

It can be presumed that there is a complex gradient (sensu Whittaker, 1967) from the forest interior through the edge to the grassland interior. Along this gradient, several environmental factors change in conjunction with one another through space. Populations are ordered along the gradient so that they form three distinct but highly inter-connected communities.

4.3. Vegetation dynamics

Currently, forest and shrubland expansion is occurring in several complex woody-herbaceous ecosystems (Archer et al., 1995), including some areas of the Pannonian ecoregion (e.g. Somodi et al., 2004; Centeri et al., 2009; Erdős et al., 2014).

In our study area, *P. alba* saplings had considerable frequency and cover values both in edge and grassland habitats (Fig. 10a), suggesting that forest encroachment is in progress. However, the analysis of aerial photographs from site B (Molnár, 2003) clearly showed that forest patches are not expanding. Moreover, Bodrogekőzy (1957) stated that saplings in edges and grasslands were unable to develop into full-grown trees, never exceeding 1 m in height. This phenomenon remained unchanged over the last fifty

years (L. Gallé, personal observation), indicating that lowland sandy forest-steppes in the southern part of the Pannonian ecoregion may be relatively stable under present conditions.

It was shown by Bodrogekőzy (1956, 1982) that soil parameters of forest and grassland patches differ highly (there is a buried forest soil beneath the forests). This difference acts as a strong inherent abiotic constraint, preventing forest encroachment into grasslands. As shown by our microclimate measurements, tree canopy and shrub layer above the edge were able to modify air temperature (Fig. 7) and air humidity (Fig. 8). It is also possible that slight alterations (e.g. humus accumulation) occurred in the soil of the edge habitat. All these modifications contributed to the formation of a distinct edge community, but they were apparently not large enough to facilitate forest expansion. Biotic alteration of the environmental factors by plants proved to promote forest expansion in earlier studies (e.g. Archer et al., 1988; Silva and Anand, 2011; Silva et al., 2013a), but in our case, such alterations are probably too weak to counteract the strong abiotic constraints. Strong inherent abiotic constraints accompanied by weak community-induced changes are expected to stabilize boundaries, resulting in a relatively stable landscape pattern over a decadal scale (Peters et al., 2006).

It is assumed that natural fires and native ungulates were responsible for limiting forest expansion during pre-human periods in northern temperate forest-steppes (Walter and Breckle, 2002). However, given the present edaphically operated stability, it seems that neither fire nor grazing is necessary to maintain current grassland proportion in our study area. Indeed, although fires have an important ecological role in many forest-grassland ecosystems, other factors (such as drought-induced tree mortality or sandy soils) may also be capable of preventing forest expansion, even in the absence of fire (Hoffmann et al., 2012).

Thus it is probable that, in the study area, the extremely high spatial variability is coupled with a surprisingly low temporal variability. Similarly, edaphic parameters proved to stabilize a grassland-sage scrub complex in California, where shrubs were unable to spread into the grassland, due to soil parameters and water availability (Hobbs, 1986). In a xeric forest-natural grassland

mosaic of the Argentinian Chaco, de Casenave et al. (1995) found lots of seedlings within the edge, which were unable to develop because of the edaphic conditions (i.e., forest expansion was inhibited). In an oak savanna of southeastern Arizona, woodland–grassland boundary is stabilized by weak seed dispersal and low seedling establishment rates, the latter caused by the lack of overstorey shade (Weltzin and McPherson, 1999).

Climate change is expected to have major effects on long-term community dynamics worldwide (Bakkenes et al., 2002; Walther et al., 2002). Responses of communities to the climate change are hard to predict (Walther et al., 2002), but it is assumed that lowland forest-steppe ecosystems of the Pannonian region are especially sensitive (Kertész and Mika, 1999; Bartha et al., 2008).

For the Pannonian ecoregion, increasing temperature and decreasing precipitation has been reported (Kertész and Mika, 1999). It is projected that the warming trend will continue, and the summer periods will be even dryer, with severe drought events (Bartholy et al., 2007; Pálfi, 2011). In our study area, these global changes are further exacerbated by regional processes, most importantly declining groundwater level (Zsákovics et al., 2007). In fact, groundwater level of the study area has dropped by 2 m during the last few decades, due to water regulation, afforestation and irrigation (Szalai, 2011).

The warmer and dryer conditions induce considerable changes in the forest-steppes. According to Molnár (2003) and Molnár et al. (2012), mortality of mature *Quercus* trees can usually be encountered. Our results add some new aspects to this observation. During our study, we found very few *Quercus* seedlings (Fig. 10c and d), but the total lack of *Quercus* saplings was even more conspicuous. As we see it, seedlings cannot develop into saplings either in the forest, or in the edge habitats. If this will be the case for a long period, *Quercus* species may disappear and the canopy will be mono-dominated by *P. alba*, as forecasted by Molnár (2003). This may be accompanied by a considerable decrease in the canopy cover, a loss of species diversity and a shift in the importance of different plant functional groups, as predicted by Kovács-Láng et al. (2000). However, it should be noted that our study concerning the cover and frequency of the main tree seedlings and saplings has serious limitations. Also, the study of Kovács-Láng et al. (2000) used a space-for-time substitution, which has considerable drawbacks. Although Bartha et al. (2008) conducted a 9-year-survey, this also proved to be too short to detect changes induced by climate change. Moreover, Bartha et al. (2008) focused on a sand grassland, disregarding forest interiors and edges. Therefore, long term analyses of the forest-steppes are needed in order to better understand how plant communities react to climatic changes.

4.4. Implications for conservation

Forest steppe remnants belong to the most threatened Pannonian vegetation types (Molnár et al., 2012). Sandy forest-steppes are at risk of complete disappearance in the upcoming decades (Molnár et al., 2012); therefore, improving our understanding on these ecosystem is crucial for establishing efficient nature conservation measures.

Our study has clearly shown that the forest-steppe consists of not two (i.e. forest and grassland), but three components, as their contact zone (the edge) is a distinct community, although it is strongly connected to both habitat interiors.

Nature conservation importance of the grassland component of the sandy forest-steppes has long been recognized. Considerable attention has been paid to sandy grassland stability, regeneration and rehabilitation (e.g. Körmöczy, 1991; Halassy, 2001; Horváth et al., 2009; Bartha et al., 2011).

In contrast, edges have been largely neglected so far in the Pannonian lowland forest-steppes. The only exception was Molnár (1998), who emphasized the nature conservation importance of the edges. Our results reinforce his view. We found that forest edges support a high species number and diversity (Fig. 5), and host several species that find their optima in edges, occurring only occasionally within habitat interiors (Table 1). In addition, the number of protected and endemic species of the edges is considerable (Fig. 2). It can be concluded that forest edges increase species and habitat diversity of the sandy forest-steppes, thus efforts should be made to gain a better knowledge on them as well as to protect their natural values.

The importance of forest patches in the conservation of the sandy forest-steppes has already been emphasized by Bartha et al. (2008, 2011), who concluded 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. We may add that forests play another important role: if the forest component is lost, the edge cannot exist any longer. This is important from a nature conservation point of view: although forest patches are usually not very rich in protected and endemic species (Fig. 2), they maintain another community type, the edge.

Unfortunately, the forest component of the sandy forest-steppes is often highly degraded or completely eliminated by human activity. This has serious consequences for edges as well, since edges are connected to habitat interiors (Fig. 4). To make things worse, regeneration of the forest is seriously damaged, probably due to dryer and warmer conditions caused by global and regional processes. The number of seedlings is low, and most tree species do not have saplings (Fig. 10). Although it is possible that natural values can be maintained even if the canopy layer undergoes a major transformation (Molnár, 2003), a considerable loss of natural values is also possible (Kovács-Láng et al., 2000). We conclude that each natural or near-natural forest patch of the Pannonian forest-steppes should be legally protected, and long-term studies should be established to monitor vegetation changes.

The Pannonian forest-steppes belong to the most complex ecosystems in Europe. Our results emphasize the conservation importance of the natural heterogeneity of the forest-steppe zone, including the forest edges as distinct communities. The present study clearly shows that every effort should be made to conserve the complexity of this ecosystem, with all of its integral components.

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