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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

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