

Is chorological symmetry observable within the forest steppe biome in Hungary? – A demonstrative analysis of floristic data

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Keywords: Distribution maps, Duna-Tisza köze, Generalized Linear Model, Quantitative plant geography, Species occurrence, Steppe biome.

Abstract: Biome interfaces are expected to exhibit chorological symmetry, i.e., decreasing trends in the number of species associated with each of the two neighbouring biomes as we progress from one into the other. Our aim was to test for such a pattern within the forest steppe biome, which is a transition zone in itself between the temperate deciduous forests and the steppe biome. Presence of chorological symmetry would provide indirect evidence for the prehuman presence of zonal steppes in the Carpathian basin. We also wished to provide an example with this analysis for drawing biogeographical conclusions based on quantitative species occurrence data, an information source hitherto neglected in Central Europe. Occurrence patterns of forest and steppe species were analysed at the Duna-Tisza köze (Danube-Tisza Interfluve) by the traditional qualitative biogeographic method and by hierarchical classification of predicted spatial pattern based on Generalized Linear Models with logistic link function. Species presences were explained by variables describing spatial orientation. In this approach, an outgroup of sand grassland species was also added to characterise the discrimination ability of the approach. The quantitative method discriminated the outgroup of sand grassland species, providing evidence of its suitability for our purpose. The results of the quantitative investigations were also in accordance with the qualitative evaluation. Surprisingly, forest and steppe species showed similar distributional patterns, i.e., no chorological symmetry was discernable. The quantitative biogeographic approach unveiled important evidence for deciding about the potential presence of zonal steppes in the Carpathian basin. Although the observed similarity of the distribution of forest and steppe species may have multiple reasons, the major cause of the lack of chorological symmetry is most probably the lack of zonal steppe South of the forest steppe biome in the Carpathian basin. Additional explanations include land use pattern and the mountain belt around the basin acting as a refugium in the ice ages.

Introduction

Biogeographical and vegetation patterns at the interface of vegetation units have long fascinated and still fascinate researchers (among others Weaver and Albertson 1956, Gosz 1993, Risser 1995, Gastner et al. 2009), since regularities of biogeographic and community pattern sharpen in these transition areas and these interfaces are expected to react first to global change (Gehrig-Fasel et al. 2007, Gastner et al. 2009). Attention has been drawn to transition areas as early as 1939, when Tansley elaborated the ecotone concept for the interface of plant communities (Tansley 1939). Later ecotones were generalised for all spatial and temporal scales including the biome interface as well (Delcourt et al. 1983, Gosz 1992, 1993, Risser 1995). While community transition zones reflect population patterns, biome transitions mirror biogeographical (species distribution) patterns. Community transitions have been extensively studied (Zólyomi 1987, Kent et al. 1997, Borhidi et al. 2003, Zalatnay and Körmöczi 2004), at the same time somewhat less attention has been paid to species distribution patterns at the margin of biomes (but see Weaver and Albertson 1956, Gosz 1993, Neilson 1993).

The transition zone of biomes is traditionally viewed as a battle ground, where the species characteristic to one or the other biome intermingle and gradually decrease towards the foreign biome (Gosz 1992, 1993), although, the gradual decrease need not to be linear (Timoney et al. 1993). If the decrease of characteristic species with distance is true for both biomes, we see a mirroring pattern of decrease in the number of characteristic species for the biome from which we start and increase of the characteristic species of the one into which we approach. With traditional biogeographic terminology we introduce the term *chorological symmetry* to denote this phenomenon. Many examples support that this pattern is general and attributable to most ecotones and biome interfaces (Gosz 1993, Camarero and Gutierrez 2002, Hennenberg et al. 2005, Peschkova and Andreyashkina 2009). A possible consequence of this pattern is an increased species richness of the ecotone, where species from both communities or biomes mix in oppositely decaying manner. Some case studies have confirmed this prediction (e.g., Shelford 1913), some others have not (e.g., Walker et al. 2003).

Chorological symmetry is believed to manifest itself with regards to the forest-steppe biome (also called wooded steppe elsewhere), since it exhibits ecotone character itself.

In Europe, forest-steppe can be found between the closed broad-leaved deciduous forests and the steppe biome. Although forest steppes have a number of transitional character, it is quite established today that to handle it as a biome on its own (Walter 1943, Berg 1958, Molnár and Kun 2000, Donita et al. 2000/2003). This biome is well distinguishable on climatic basis, primarily on the length of the summer arid period. The westernmost occurrence of the truly climatic-driven, well developed forest steppe biome can be found in Hungary, as a part of the so-called submediterranean forest-steppe, a specific version of the biome in Southeastern Europe (Niklfeld 1973, Horvat et al. 1974, Ivan et al. 1993, Bohn et al. 2000/2003). In the Carpathian basin, the zone of closed forests clearly accompanies the mosaic-like forests of the forest-steppe (Zólyomi 1967). To find zonal steppes, however, is more difficult. There is even ground for debates whether this biome was ever present in the Carpathian basin as such (Zólyomi 1953, Krolopp 1995, Magyarai 2002, Járαι-Komlódi 2003).

In Central Europe (Lepší and Lepší 2006, Purger et al. 2008), but specifically in Hungary (e.g., Csiky 2005, Barina 2006, Nagy 2007, Somlyay and Bauer 2007, Bauer et al. 2008) there has been a recent boom in collecting species occurrence (floristic) data. Nevertheless, these data are at most used to identify local biogeographic patterns and attempts to synthesise and draw more general conclusions based on quantitative area investigations are relatively sparse (Chytrý et al. 1999, Finnie et al. 2007, Sólomos 2008, Kozłowski et al. 2009). Also, phytosociological databases (Chytrý and Rafajova 2002, the CoenoDat database in Hungary) are potential sources of species occurrence data and are not used extensively in this sense. However, species occurrences provide useful information for modelling climate change effects (Pearman et al., 2008, Randin et al. 2009), but also for understanding larger-scale biogeographic pattern (Finnie et al. 2007, Kozłowski et al. 2009).

In this paper, we aimed at testing for the presence of chorological symmetry of forest and steppe species in a region of Hungary belonging to the forest steppe biome. This test was also intended to provide indirect evidence for or against the presence of zonal steppes in the Carpathian basin. We hypothesized that the frequency of forest species will decay to the south along the climatic and prehuman vegetation gradient, while steppe species will become more frequent if

there has been a zonal steppe present. Besides, we also set the goal of providing an example of drawing biogeographical conclusions based on floristic data. Such data are available for Central Europe and specifically for Hungary in vast numbers but have been neglected so far.

Methods

Study area

We investigated the distribution of steppe and forest specialist species in a separate part of the Great Hungarian Plain bordered by two rivers called Danube-Tisza Interfluvium (Danube-Tisza Köze in Hungarian). The Danube-Tisza Interfluvium is bordered by the Gödöllő-hills to the North, and the limit of our investigations was the country border to the South (Fig. 1). There is a North-South climate gradient in the region: mean annual temperature ranges from 10°C in the North to 11°C in the South. Mean annual precipitation is more evenly distributed: typically 600 mm per year, but the central-eastern part receives only 550 mm per year (Borhidi 1993). Statistical climate investigations, which were based on the climatic year concept (Köppen 1929), show that in the middle of the Great Hungarian Plain, on both sides of the river Tisza the frequency of the so-called steppe years reaches its maximum (Borhidi 1993). The climate gradient is reflected in the likely prehuman vegetation distribution of the area. The substrate supported forest steppe climatic climax vegetation (Zólyomi 1967). However, the structure of the vegetation gradually changes from North to the South shifting from higher to lower forest cover (Kovács-Láng et al. 2000). The bedrock of the region is predominantly loess and sand (Pécsi and Sárfalvi 1965).

Detailed description of the floristic characteristics of the study area can be found in Fekete et al. (1999, 2008). Nomenclature follows Tutin et al. (1964-1993).

Data

Our investigations were primarily based on floristic data comprised in Szujkó-Lacza and Kovács (1993), which is a synthesis of species occurrences in the region based on archive sources from the 18th century, exemplars found in herbaria and recent data up to the publication date. We extended the information in this synthesis by additional actual data in the phytosociological database of the Institute of Ecology and Botany of the Hungarian Academy of Sciences (CoenoDat).

The forest steppe in the Carpathian basin is a fine-grained mixture of wooded and open, steppe-like patches. In this study, we used species characteristic to the grassland and forest components of the forest steppe, the former group occurring in the steppe, the latter occurring in the forested biome as well. Species reflecting edaphic conditions were excluded except for species preferring open grasslands on sand substrate. These were included among the grassland species, so that they would form a distinct outgroup. Sand substrates have an apparent geographic pattern in the region at the same

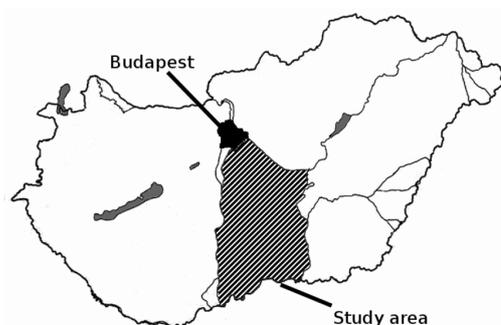


Figure 1. The region of Duna-Tisza köze, the study area.

time they have a specific flora which does not overlap with the forest or steppe flora. We applied the sand grassland group as an independent indicator of the discrimination ability of our approaches regarding spatial pattern.

Species occurrences were resampled at the scale of the Central European Flora Mapping Grid (Niklfeld 1971), because the description of the localities would not allow a more precise localisation. At the same time, this resampling also offered a regular distribution of the available information in space. The cell size of the Central European Flora Mapping Grid is 10 km by 13 km and there have been 15 cells in the North-South direction (150 km) and 8 in the East-West (104 km). Species which were present in less than 5 cells of this grid have been omitted.

There were 243 species selected altogether for the study (103 forest, 110 steppe and 30 sand species). As a guide in the allocation of individual species to these three groups, we used the classification of Simon (2000) apart from a few exceptions, where we followed our field experience.

Analyses

Distribution pattern was first qualitatively assessed based on the distribution maps, an approach corresponding to the traditional biogeographic evaluation.

To provide a quantitative assessment of the spatial occurrence pattern of the individual species we used predictions of Generalized Linear Models (GLM) built with logistic link function (McCullagh and Nelder 1983) in the R statistical environment (R Development Core Team 2008). The predictions quasi reconstruct the local biogeographic area for each species. In the models the response variable was the presence/absence pattern of each species separately, explanatory variables were those describing spatial orientation corresponding to possible gradients: East-West (x), North-South (y), these at the second power (x^2 , y^2) as well as their interaction ($x:y$). Second powers were included to be able to capture non-linear pattern as well. These models were applied to the full study area so as to produce probability predictions for each cell. Then species were classified based on their co-occurrence patterns as predicted for the cells of the Central European Flora Mapping Grid.

We used the “hclust” function of R software with the “average” option, which corresponds to the group average technique and Euclidean distance (R Development Core Team 2008).

Results

Qualitative assessment of local areas

Four major groups can be distinguished among forest species according to the degree they penetrate towards the South.

1. Species only present in the northern third of the Danube-Tisza Interfluve. Specialist species, such as *Lychnis*

coronaria, *Dictamnus albus* (Fig. 2a). 12.6% of the forest species in the study.

2. Species that reach the middle of the region: e.g., *Viburnum lantana*, *Doronicum hungaricum* (Fig. 2b). The most common pattern among forest species: 41.2%.

3. Species absent from in the southern third of the area and especially rare in the centre of the region. (*Silene nutans*, *Buglossoides purpureocaerulea*, Fig. 2c), 29.4%.

4. Species uniformly and densely distributed in the area, without apparent gradients. These are the forest generalists, such as *Crataegus monogyna*, *Hieracium umbellatum* (Fig. 2d), 16.8%.

Three groups emerge if we investigate the spatial pattern of the steppe species. (Sand grassland species were not included into the qualitative investigations.) These are

1. Species present in the northern third or half of the area (e.g., *Dorycnium pentaphyllum* subsp. *germanicum*, *Trinia glauca*, *Hesperis tristis*, Fig. 3a). Typically rare species, also a gradient of decreasing presence can be seen southwards. When investigating the group from a phytosociological point of view, the component species appear to be dry grassland specialists and indicator species. This group comprises 30% of the steppe grassland species involved in the study.

2. Species occurring in the whole Interfluve, but more frequent in the North. These are also rather rare species (pl. *Seseli pallasii*, *Hieracium echioides*, *Veronica paniculata*, Fig. 3b), 11%.

3. Evenly distributed species (e.g., *Asperula cynanchica*, *Linaria genistifolia*, Fig. 3c). Often dominants or co-dominants in the grasslands of the forest steppes or steppes. 59% of grassland species in the study.

It is quite striking from this visual interpretation that the specialist species of the steppe and forest flora show common distribution pattern as they tend to concentrate in the northern part. Furthermore, a southward decreasing gradient can also be identified for them. It should be emphasized that no species bound exclusively to the southern part of the region can be found either among the forest or the steppe plants. A moderate concentration to the South is observable in the case of a few widespread species only (e.g., *Cephalanthera rubra*, *Epipactis atrorubens*, *Epipactis helleborine*, *Jurinea mollis*, *Minuartia glomerata*), and distributional patterns with dual centers (North and South) are rare as well (*Odontites lutea*, *Orchis purpurea*, *Rosa pimpinellifolia*, *Viola ambigua*, *Viola odorata*).

Classification based on logistic regression

These tendencies also show up clearly on the dendrogram that results from the hierarchical classification (Fig 4, see Appendix 1 for explanation). Species characteristic to the northern part of the region and decreasing Southwards (shortly: northern species, species typed in bold in the Appendix) are concentrated overwhelmingly in a large cluster

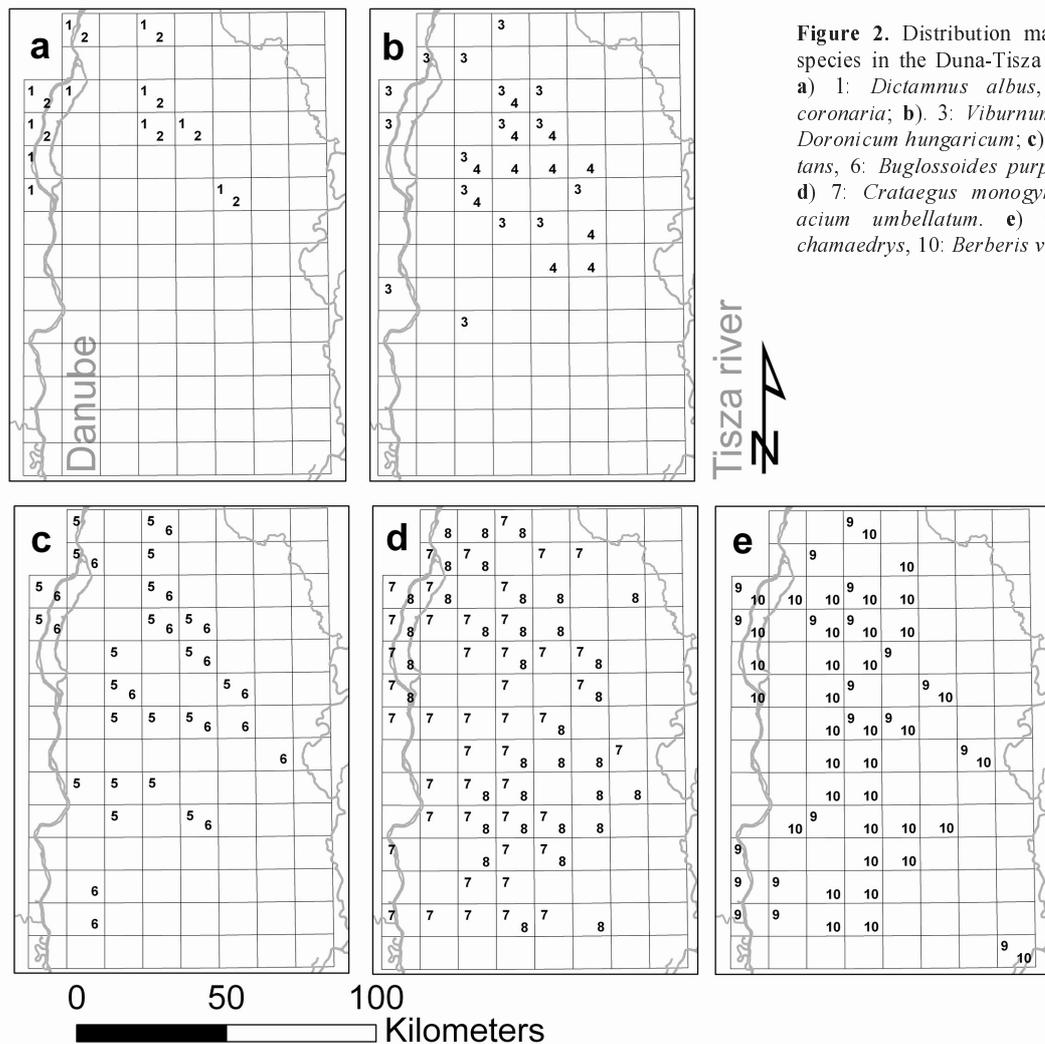


Figure 2. Distribution maps of forest species in the Duna-Tisza köze region. **a)** 1: *Dictamnus albus*, 2: *Lychnis coronaria*; **b)** 3: *Viburnum lantana*, 4: *Doronicum hungaricum*; **c)** 5: *Silene nutans*, 6: *Buglossoides purpureocaerulea*; **d)** 7: *Crataegus monogyna*, 8: *Hieracium umbellatum*. **e)** 9: *Veronica chamaedrys*, 10: *Berberis vulgaris*.

(from species 143 to 240). These are clearly separated from other parts of the dendrogram. The most important finding is that the group of northern species contains forest and steppe plants alike. Actually, these are the habitat specialists both among forest and steppe species, which was also a characteristic that divided species groups based on local areas in the qualitative analyses as well.

For some species, a more pronounced West-East tendency can be observed in the field distribution (e.g. Fig. 2a&c, but especially pronounced in Fig. 2e). This pattern is somewhat more frequent among forest plants than steppe plants. Also, differences along the West-East gradient are more pronounced among forest species they typically become rarer eastwards. The West-East distribution pattern is sometimes connected with a North-South gradient, some of these species (*Moehringia trinervia*, *Rosa corymbifera*, *Globularia punctata*, *Lapsana communis*, *Acer campestre*, *Peucedanum alsaticum*, *Festuca gigantea*, *Clematis recta* and *Linum flavum*) are situated close to each other in the dendrogram (see 151 to 162 in the species order, Appendix).

A group of species with dual centers (in the northern and southern part of the region) mentioned in the qualitative section can be also recognized as a result of the classification (from species 235 to 239).

Our outgroup, the sand species are mostly separated from the other species, in three larger groups and a few one-three species groups. This pattern can be explained by their preferences to different minor regions with sandy soil within the Danube-Tisza Interfluve, which are isolated from each other to some degree. The fact that the sand species are less mixed with the forest and steppe species than those among each other, proves that the mixing of steppe and forest species is not due to the inability of our method to differentiate among spatially differently behaving groups.

In concordance with our qualitative evaluation, it could be stated that the distribution of the species with a small local area (and habitat specialists at the same time) are generally well explained by a decreasing tendency along the north-south gradient.

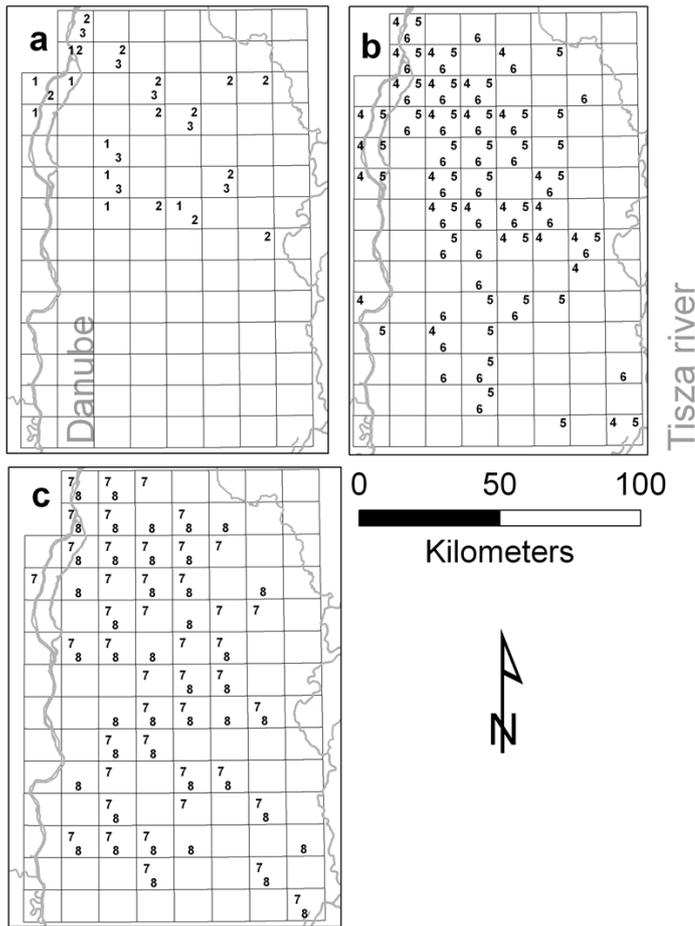


Figure 3. Distribution maps of steppe species in the Duna-Tisza köze region. **a)** 1. *Dorycnium pentaphyllum* subsp. *germanicum*, 2. *Hesperis tristis*, 3. *Trinia glauca*; **b)** 4: *Seseli pallasii*, 5: *Hieracium echinoides*, 6: *Veronica paniculata*, **c)** 7: *Linaria genistifolia*, 8: *Asperula cynanchica*.

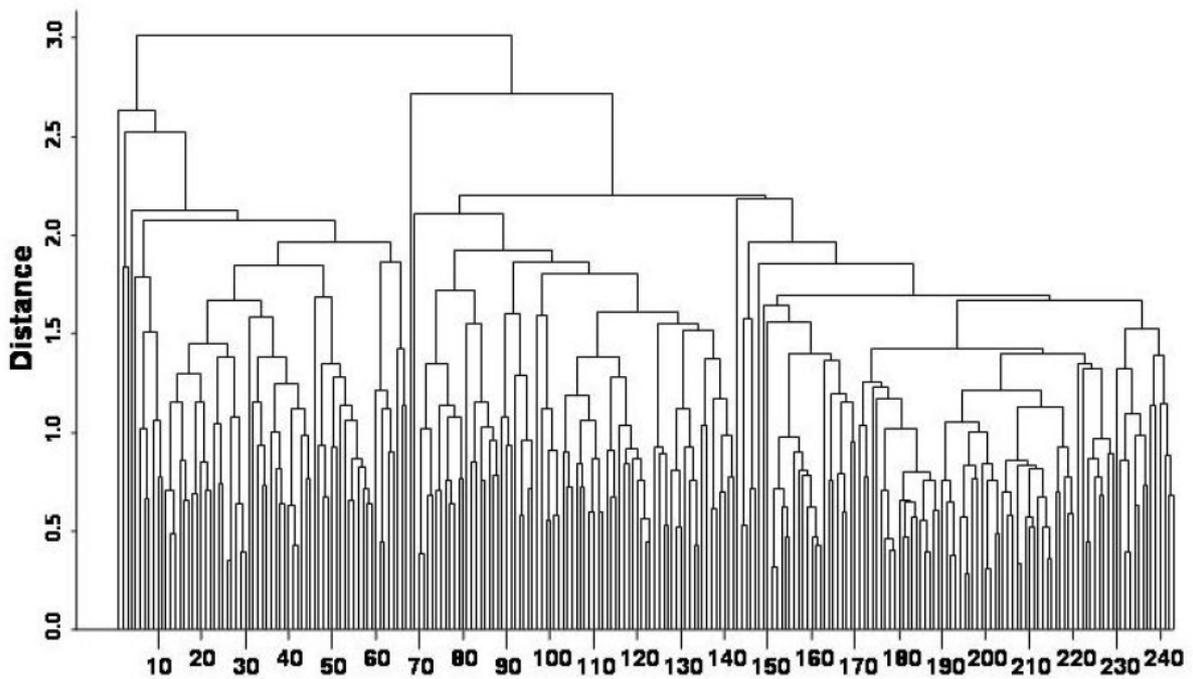


Figure 4. Hierarchical clustering of species (based on Euclidean distances, group average technique). Appendix contains the explanation of the species groups identified in the dendrogram.

Discussion

As our statistical approach was able to quantify and characterise spatial pattern of local areas corresponding to traditional biogeographic area evaluation, we believe that the approach introduced here will provoke thoughts about utilising all the rich floristic sources that are available for Central Europe, but have at most been analysed according to the qualitative method (e.g., Csiky 2005, Barina 2006, Nagy 2007).

We found no chorological symmetry for forest and steppe species in the Danube-Tisza Interfluvium, however. Generalist species were evenly distributed, while specialist species decayed southwards, irrespective whether they belonged to the forest or the steppe group. As a contrast, sand species did not follow this pattern, as they showed an almost exclusive preference in the substrate offering semidesert-like conditions. All authors concerned with biome interfaces so far found signs of chorological symmetry (Gosz 1992, 1993, Timoney et al. 1993, Camarero and Gutierrez 2002, Hennenberg et al. 2005, Peschkova and Andreyashkina 2009). Specifically for the forest-steppe biome (as interface between forest and steppe biomes) chorological symmetry is apparent from the distribution of plant species in Ukraine (Barbaric et al. 1986). Therefore we would expect the same if a zonal steppe had accompanied the submediterranean forest-steppe in the Carpathian basin as well. There are multiple possible reasons, why we could not find signs of this, some of which relate to land use history, some of which are biogeographic reasons.

The major historic factor that might hinder the detection of chorological symmetry in the region is the intensive agriculture. Actually, agriculture is more and more intensive towards the south with a most intensive core in the middle of the basin (Bíró et al. 2008). This pattern is generally reflected in the decrease of specialist species southwards. It is likely, however, that agricultural use in the ancient time has affected forests more than grasslands. This could be a reason, why forest species become rarer towards the South, but does not explain why steppe species exhibited the same pattern. This biased use of forests in the South would have favoured the survival of steppe species there.

Therefore, the pattern found is most likely to be explained by biogeographic causes, the lack of a steppe zone along the submediterranean forest steppe to the south. The opinions in this respect are contradictory. Botanists and paleoecologists (Zólyomi 1953, Krolopp 1995, Járαι-Komlódi 2003) assumed that steppe vegetation obtained its largest distribution in the warm and arid Boreal period of the Holocene, so that the central part of the Great Hungarian Plain became covered by steppe. The patches of the xerotherm grasslands in the Great Hungarian Plain in the present can be interpreted according to Zólyomi as partly transformed, last remnants having their origin in the Boreal period.

On the other hand, Magyari et al. (2010) debate the existence of extensive xerotherm grasslands in the Boreal period. Kordos (1987), Magyari (2002) and Magyari et al.

(2010) emphasize that steppe fragments of the early Holocene started to be used for mild agriculture so early that the late Holocene forest-steppe expansion has been halted by humans. The human-maintained steppes did not form a zone, therefore though they preserved steppe species, the chorological pattern of those does not correspond to that at the interface of biomes.

Furthermore, the presence of steppe species in the forest steppe zone is not even necessarily due to steppe patches maintained by human activities through the Holocene. The submediterranean (Pannonic-Balcanic) forest steppe has a different structure than the eastern European – Asian type. While the latter is composed of large patches of closed forest and steppe grasslands (Berg 1958), the submediterranean forest-steppe is a fine-grain mosaic of wooded patches and clearings (Jakucs 1961). The wooded patches themselves are much more open than those of the eastern forest steppe, which allows a rich ground layer to establish, where steppe species also find their place (Molnár and Kun 2000). Therefore, the submediterranean forest steppe contains both forest and steppe species (Zólyomi 1957, Zólyomi and Fekete 1994).

Although this first biogeographic explanation detailed so far tells us why forest and steppe species distributions follow the same pattern, it does not explain why specialist species of both kind become rare southwards.

There might be a second biogeographic reason for this. Forest-steppes are in a specific position in the Carpathian basin. Unlike the lowlands in Eastern Europe, the Great Hungarian Plain is surrounded by mountains, which limit the expansion of drought-tolerant biomes. At the same time, during the ice ages the slopes of the lower mountains could provide a refugia for the warm-demanding steppe and forest-steppe species (Zólyomi 1958). Mountains are closer to the region investigated in the North than in any other direction, therefore it is reasonable that more species could reach the North of the region, when the climate warmed again. This also explains the gradual decay of specialist species presence southwards. Furthermore, the second closest mountain region, where there are stands of the forest biome is located to the West. This explains well, why a West-East and/or a diagonal Northwest-Southeast gradient was also discernable, especially for many forest species.

To sum up, the lack of chorological symmetry in the Interfluvium regarding forest and steppe species is mainly due to biogeographic reasons. The major factor is the most probable lack of a zonal steppe south to the forest steppe biome in the region investigated. The steppe species observed in the Danube-Tisza Interfluvium were components of the prehuman forest steppes or were preserved by human land use rather than being remnants of zonal steppes.

The southwards decaying trend in specialist species, however, can be linked partly to a local biogeographic pattern: the surrounding mountains having offered refugia to drought-tolerants in the ice ages; partly to land use pattern: the southern parts were more heavily used for agriculture.

Acknowledgements. We are grateful to F. Horváth for his technical help in preparing the distribution maps. We also thank S. Bartha and Z. Botta-Dukát for their useful comments on the manuscript. I. Somodi has been supported by the Hungarian Research Fund (OTKA) grant no. NI 68218.

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Received November 23, 2009
 Revised March 22, 2010, April 8, 2010
 Accepted May 11, 2010

Appendix

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