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Different impacts of moderate human land use on the plant biodiversity of the characteristic Pannonian habitat complexes

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Abstract

Habitat complexes exhibit varying vulnerability to human land use and thus have different impacts on biodiversity. In this study, we analyzed the effect of moderate land use on the plant species diversity in six characteristic Pannonian habitat complexes: forest steppe complex on sand, on dolomite, and on loess, as well as alkaline habitat complex, freshwater marsh complex, and zonal broadleaf colline forest. We chose two regions for each complex, and in each region, we selected a 2 x 2 km "natural" study site in a mostly protected area, and a moderately used "managed" site of the same size. We compared the alpha, beta, and gamma diversities of the total and the specialist species pools of the natural-managed site pairs by applying stratified random sampling and novel bootstrap statistics.

The gamma diversity of the specialist species pool was found to be the most sensitive indicator of naturalness. It was higher in the natural sites of the loess and dolomite forest steppe and the freshwater marshland complexes, while there were no significant diversity differences in the other complexes. The diversity comparisons showed a consistent pattern: there were either no significant diversity differences in any of the natural-managed pairs, or there were significant differences in the gamma diversities of the specialist species pool in both the natural-managed pairs.

We concluded that the same differences in naturalness may represent different sensitivities to human management as characterized by differences in diversity measures. Three habitat complexes, the loess and dolomite forest steppe and the freshwater marshland, require more focused nature protection efforts in order to preserve the habitat diversity, especially in maintaining the remnants of the natural woody patches and the most inundated habitats of the marshlands. In the case of the other studied complexes, moderate human land use can be harmonized by nature protection goals.

Keywords

Naturalness; Land use; Gamma diversity; Specialist species; Bootstrap method;

Nomenclature: Simon (2000)

Geographical names: Kocsis (2018), page 126

1. Introduction

The increase in human land use is causing a global decline of biodiversity (Butchart et al., 2010; Hoekstra et al., 2005). Besides regional and global drivers, the consequences of local land use decisions are major factors of this global decline (Foley et al., 2005). Studies on human land use and biodiversity relations are important for both theoretical and practical reasons (Cardinale et al., 2012). A growing body of knowledge on these relations is being generated from experiments, large scale research, and case studies (Hudson et al., 2014). So far, the results are too diverse for general predictions concerning nature protection. Moreover, different biotic communities of varying scales react differently to human impact (McGill et al., 2015).

On most parts of the Earth, especially in the temperate climate zones, only small patches with more or less natural biotic communities are left in the matrix of areas that are exposed to variably intense land use. Out of these areas, the wilderness that are often not strictly protected should be safeguarded as an important element for maintaining biodiversity (Mittermeier et al., 2003). While the protection of the biodiversity hotspots is particularly important, it may not be enough if the wilderness around the hotspots are degrading (Mittermeier et al., 2011).

Low intensity land use does not necessarily lead to local decrease of biodiversity (Newbold et al., 2015). In Central and Eastern Europe, the rural landscape is a major contributor to the regional biodiversity, more so than in the more urbanized Western Europe (Palang et al., 2006). According to national mapping of natural capital, the moderately altered rural landscapes have essentially contributed to the naturalness of the country (Czúcz et al., 2008).

Human impact causes a decrease in the naturalness of various habitat complexes, which may result in a loss in biodiversity (Dengler et al., 2014; Wallenius et al., 2010). We were interested in how the decrease in naturalness and changes in biodiversity are related at the landscape level. Our aim was to study the impact of moderate land use on the diversity of the most characteristic natural habitat complexes of the Pannonian biogeographical region. However, no comparative studies exist on moderate human impact on the major habitat complex types of high biodiversity value in Hungary. Although many studies deal with the effect of human impact on certain components of biodiversity (e.g. Biró et al., 2008; Botta-Dukát, 2008; Csaba et al., 2015; Csontos et al., 2012; Deák et al., 2016; Molnár et al., 2012; Somodi et al., 2004; Standovár et al., 2006; Tóth and Kertész, 1993), the scale of habitat complexes is beyond the scope of these studies. We intend to provide a reliable estimation of the impact of the moderate intensity human management to the most characteristic natural habitat complexes of Hungary. We chose the diversity of the vascular plants as a biodiversity indicator and six habitat complexes to represent the major habitat types of the Pannonian biogeographical region (Zólyomi, 1989). We also aim to compare the diversities of the specialist species separately because we assume these would provide more relevant information on the impact of human management (Clavel et al., 2011; Naaf and Wulf, 2010)..

In this paper, we put forward the following research questions: 1) Do the pairs of natural-managed habitat complexes differ based on alpha, beta, and gamma diversity indices? 2) Do the diversity indices calculated by specialist species respond differently to the level of human management than those of the total species? In order to assess the impact of humans on landscape scale diversity, with regard to both the actual plot scale diversity and the area of habitat types, we used a novel application of bootstrap on a stratified relevé sample. Our general null hypothesis was that there was no difference between the natural and corresponding managed pairs in the diversity estimations.

2. Materials and methods

2.1. Habitat complexes

We chose six characteristic habitat complexes of Hungary for our study (Zólyomi, 1989). Four of them were edaphic variations of the forest-steppe biome, namely forest-steppe developed on loess, dolomite, and sand substrate and on alkaline soils (Molnár et al., 2012), as well as the formerly much more extended lowland marsh habitat complex (Zólyomi, 1989; Varga et al., 2013), and finally, the most widespread quasi natural habitat type of the country, the low- and mid-range mountain forests (Bölöni et al., 2008). For each habitat complex we selected two natural–managed site pairs to compare their alpha, beta, and gamma plant species diversity.

The major characteristics of the natural and managed sites (see 2.2) of the six selected habitat complexes are summarized in Table 1.

Table 1. The six characteristic habitat complexes that represent a majority of the natural habitats in Hungary.

Habitat complex	Natural	Managed
Forest-steppe complex on loess	Xeric and xero-mesic lowland or slope steppes, forest fringes, shrubs, and mixed oak forests on loess.	Fragmented loess pastures with a reduced forest component
Forest-steppe complex on dolomite	Open and closed rock grasslands, slope steppes, open and closed oak, and mixed woodlands on dolomite.	Grazed dolomite grasslands without a natural forest component
Forest-steppe complex on calcareous sand soil	Open and closed grasslands and oak and juniper-poplar steppe woodlands on sand soil.	Pastures with reduced natural forest components on sand soil
Alkaline habitat complex	Inland alkaline turbid lakes, saltmarshes, alkaline meadows, and alkaline steppes.	Grazed or mown alkaline wetlands and pastures
Freshwater marsh complex	Lowland marshes or bogs, wet meadows, and wet woodlands.	Grazed or mown freshwater wetlands with reduced regularly inundated areas
Complex of zonal colline forests	Pannonian beech, oak-hornbeam, turkey oak-sessile oak, mixed ravine or slope forests, and rock grasslands.	Forests of indigenous tree species subject of even-aged timber management with secondary grassland patches

2.1.1. Forest-steppe complex on loess

Fragments of the forest steppe on loess areas survived to larger extent on the southern slopes of the Transdanubian Range and North Hungarian Range, where the relief limited the extent of intensive agriculture (Erdős et al., 2014; Illyés and Bölöni, 2007). Several areas had been utilized as vineyards until the end of the 19th century and then were grazed with varying intensity. In order to maintain the pastures, woody vegetation in large areas were cut down. The slopes with deep soils were often covered by woody vegetation, while on the heavily eroded surface rocks, grasslands formed. Such a complex can be extremely rich in plant species and can serve as an important refuge for several endangered forest steppe species of the Pannonian region (Molnár et al., 2012).

2.1.2 Forest-steppe complex on dolomite

This habitat complex appears in the largest extent on the Transdanubian Range. The rich relief and limited soil formation result in a fine scale mosaic of edaphic habitats with considerable richness in endemic and specialist species at the edge of their distribution range (Zólyomi, 1958; Debreczy, 1987). This mosaic consists of open rock grasslands and slope steppes, closed rock grasslands on the top of the northern slopes, and woody vegetation in the depressions and the lower parts of the slopes with deeper soils. In the southern exposition and the northern slopes, termophilous dry open oak woodlands and mesic ravine forest types are typical, respectively. Traditionally, the land is used for grazing sheep; therefore, the extent of woody vegetation has reduced (Báldi et al., 2013).

2.1.3. Forest-steppe complex on calcareous sand

This habitat complex is mostly found in the Danube-Tisza Midland Ridge of the Kiskunság region in Central Hungary. The extreme moisture regime of the coarse sand, the rich relief, and the transitional forest-steppe climate of the region has resulted in a fine scale mosaic of dry sandy grasslands, open oak and juniper-poplar woodlands, and closed oak or poplar forests (Kertész et al., 1993). Woody habitats are relatively species poor in comparison to grasslands, which are rich in endemic species (Rédei et al., 2014). The land was traditionally used mostly for grazing cattle and sheep. With the intensification of land use, rich soils of the lowest elevation had been ploughed, and extended tree plantations had been established. The Kiskunság region has suffered a significant decrease in the soil water table over the last decades, which has led to significant degradation in the natural/semi-natural vegetation (Biró et al., 2008).

2.1.4. Alkaline habitat complex

Alkaline vegetation is widespread in the lowland areas of the Great Hungarian Plain (Molnár and Borhidi, 2003). The composition of vegetation is determined by the distance of the vegetation from the soil water table. A few centimeters of difference can change the vegetation and result in a fine scale mosaic (Deák et al., 2014; Tóth and Rajkai, 1994). In depressions with long-time yearly water cover, alkaline marshes and alkaline wet meadows dominate. Near the soil water table, annual alkaline mud vegetation and *Puccinellia limosa* swards appear. A few centimeters higher, alkaline steppe grasslands dominate. Their species pool contains several Pontic and Pontic-Pannonian elements, which confirm the long-time presence of the complex in the region. At the highest level, isolated steppe grassland patches mosaic with the alkaline vegetation; their character is determined by the substrate. However, the abiotic stress strongly limits the species pool (Török et al., 2012). When the soil water table decreases significantly, the alkaline character disappears, and the species poor dry grassland substitutes the alkaline vegetation (Bagi, 1988).

Traditionally, the land is dominantly used for grazing by cattle on the deeper end and by sheep on higher elevation (Báldi et al., 2013).

2.1.5. Freshwater marsh complex

Before the river regulations and artificial drainage campaigns in the 19th century, a large part of the Great Hungarian Plain was covered by different wetland complexes (Biró et al., 2018; Schweitzer, 2009; Verhoeven, 2014). The freshwater wetland types were either alluvial or groundwater based. On the alluvial terrains of the large rivers, the continental types of the eutrophic wet meadows were dominated with riverine willow scrubs, reed beds, and tall herb vegetation. Moreover, dryer areas are covered with mesic pastures and hay meadows. The intensively changing water regime limits the plant species pool of this region. On groundwater-based wetlands, rich fens and oligotrophic meadows dominate. Willow scrubs and oligotrophic tall herb vegetation are found at lower elevations, while, on higher areas, steppe grasslands substitute the meadows. The natural mosaic of wet and dry grasslands result in high species diversity (Molnár et al., 2008). A main factor behind the degradation is the decrease in soil water table, when secondary mesic and dry grasslands appear, with significantly less species richness (Biró et al., 2013). Traditionally, the land is use for mowing and grazing cattle along with controlling the woody vegetation.

2.1.6. Complex of zonal colline forests

Deciduous forests constitute the zonal vegetation in the colline and mid-range regions of the Pannonian basin (Trandanubian Range, Transdanubian Hills, and North Hungarian Range) (Zólyomi, 1989; Bölöni et al., 2008). Sessile oak dominates the elevation between 200 and 500 m, while European beech prevail above this level. Sessile oak is mixed with turkey oak on dryer plateaus and southern slopes and with European hornbeam in more humid habitats. On shallow soils, mixed ravine and rock debris forests grow. On peaks and ridges in the southern exposition, small patches of rock grasslands, slope steppes, and scrublands increase the diversity of the habitats. In smaller areas where drainage is poor, fens and meadows may appear. Furthermore, small watercourses are tied with thin gallery forest belts. In the whole region, even-aged timber management is the norm (Lett et al., 2016); thus, more or less natural stands with a mixed age structure and tree species composition are very rare. Locally, alien spruce, black pine, and Scots pine may have been planted to a considerable extent.

2.2. Selection of study sites

We used the database of the MÉTA habitat mapping project (Molnár et al., 2007) for selecting the location of the study sites. The database is the result of a national habitat mapping project, a collaborative effort of more than 200 botanists who spent more than 7,000 workdays on the field. The surveyors recorded the natural and semi-natural vegetation types in 260,000 hexagons of 0.35 km^2 by applying the MÉTA habitat classification system (Bölöni et al., 2011) with the help of satellite images, airborne photographs, as well as actual and historical topographical maps. Beyond vegetation types, naturalness was also estimated on a 1–5 point scale (1 – totally degraded state; 5 – natural state) as well as some additional variables, such as the presence of alien invasive plants species.

Although the database consisted of habitat records from hexagons of 0.35 km^2, which limited the spatial resolution, the area ratios of different habitats, characterized by vegetation types and naturalness indices, were provided for each hexagon. The aim of the study site selection process was to represent the diversity of the habitat complexes in the region. We intended to apply the criteria as follows: a) 80% of the area of "natural" site should be covered by vegetation types that belong to the studied habitat complex and are characterized by a high naturalness index (4 – semi-natural state; 5 – natural state); b) 80% of the area of "managed" sites should be covered by vegetation types that belong to the studied habitat complex and are characterized by a medium naturalness index (3 – moderately degraded state); c) the study sites should contain as many suitable habitat types as possible; d) the members of the natural–managed pairs should be share similarities in basic geographic features and should be close to each other.

However, all the selection criteria could not be accommodated; the 2 x 2 km size of the study sites was the largest one where a majority of the requirements could be met. A reason for the difficulties in selecting and positioning the study sites was that the patches of the "natural" quality habitat complexes were small and isolated. In the case of the forest-steppe complex on loess, the cover varied between 32% and 68%. As for the forest-steppe complex on dolomite (see Table A1), the members of one of the natural–managed pairs (Csákvár-Zalahaláp) were close to the opposite ends of the Transdanubian Range. (Fig. 1, pair D2). For choosing between appropriate sites and for exact positioning, expert decisions were sought.

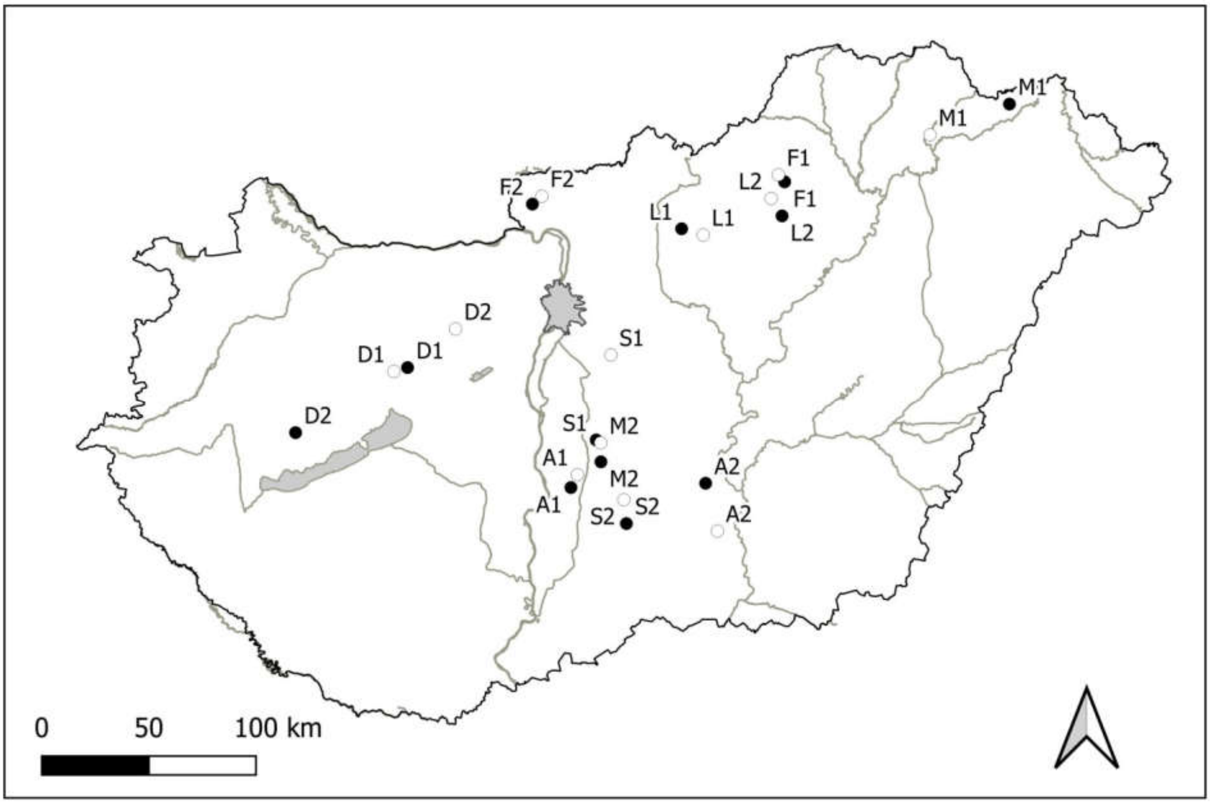

Figure 1.

2.3. Determination of habitat type areas

We also used the database of the MÉTA habitat mapping project for assessing the proportion of each sampled habitat that is relative to the 2 x 2 km study sites. For this purpose, we chose 13 hexagons of 0.35 km^2 from the MÉTA database that occupied the largest parts of the study sites. These hexagons provided information on the extent of the habitats that covered 90 percent of the sites on average without covering considerable areas of the surroundings, and we extrapolated the summarized habitat ratios of the hexagons to the whole sites. The application of more hexagons that covered areas beyond the sites was not a viable option because of the careful positioning of the borders of the sites.

2.4. Selection of plots

For recording relevés, we chose a 20 x 20 m plot size. The first step of the selection of plots was to compile a concise list of habitat types for each study site based on the MÉTA habitat mapping data and preliminary field survey, which resulted in 6 to 13 habitat types per habitat complex and 4 to 11 types per study site (see Table A1). Only the habitats with 3, 4, or 5 naturalness indices were taken into account. Each habitat type was sampled by a maximum of 3 plots. The plots of a given habitat type were placed in a separate patch or at a minimum of 200 m away from each other in larger patches. If there was no opportunity to place three plots in the above manner because the habitat type occurred only in one or two small patches, we placed only one or two plots in the given habitat type. The exact positions were randomly chosen based on high resolution multicolor aerial photographs. The quality of the aerial photos was good enough to avoid vegetation type boundaries inside sampling units. The placing of the quadrats were adjusted on the field, if necessary, in order to avoid roads or other intensive local anthropogenic disturbances.

2.5. Sampling

The percentage covers of the vascular plant species were recorded in the relevés. The exact position of the plots was determined by GPS in the field. The sampling was carried out between 2007 and 2012 (See Appendix III).

2.6. Statistical evaluation

The number of species, the simplest and most widely used diversity measure was chosen. Thus, alpha diversity is the mean richness of a randomly selected plot, gamma diversity is the number of species in a pooled species list of several plots, and beta diversity is the ratio of gamma and alpha diversity. The unit of alpha and gamma diversity is the number of species, while the unit of beta diversity is the number of maximally distinct communities (Jost, 2007; Tuomisto, 2010).

The observed gamma diversity strongly depends on sampling intensity, i.e., the number of plots (Gotelli and Colwell, 2001). There are two approaches to correct possible problems that emerge when estimates with different sampling intensities are compared: extrapolation (Colwell and Coddington, 1994; Palmer, 1990) and rarefaction (Chiarucci et al., 2008). Extrapolation methods assume that the species composition (at least roughly) is homogeneous, i.e., the probability of occurrence of a given species is the same in each plot, which is clearly not satisfied for our habitat complexes. Chao et al. (2000) developed a method for extrapolating richness in two communities and their shared species. In case of a habitat complex comprising only two habitats, the sum of the two extrapolated richness minus the extrapolated number of shared species results in the extrapolated richness. Unfortunately, this cannot be generalized to cases with three or more habitat types, where the number of the shared species should be estimated for not only pairs, but also triplets, quadruplets, etc., of habitats.

Incidence-based rarefaction provides the expected numbers of species observed in a given number of plots when the plots are randomly drawn without replacement (Colwell et al., 2004; Colwell and Coddington, 1994). It can be done easily by randomization; however, analytical solution is also a possibility (Chiarucci et al., 2008; Mao et al., 2005). While analytical solution assumes environmental homogeneity, random re-sampling does not.

In the simplest re-sampling scheme, each plot is drawn with the same probability. In an appropriate re-sampling scheme, the original sample comes from random sampling. However, in a heterogeneous landscape, stratified random sampling is more appropriate than complete random sampling since the latter easily misses the rare habitat types. We had conducted stratified random sampling in the field; therefore, we could not apply complete random re-sampling. Instead, we applied bootstrap re-sampling where the probability of drawing each plot is proportional to the area of habitat it belongs to divided by the number of plots in that habitat type. In this way, the proportions of the habitats in the bootstrap samples were approximate to the proportions of habitats in the landscape (and may have differed from their proportion in the original sample, where the rare types were over-represented). The size of the bootstrap sample was set to the lower sample size in the habitat complex pair. Bootstrapping means re-sampling with replacement, while in traditional rarefaction, plots are drawn without replacement. We did not apply drawing without replacement because, in this approach, the proportions of habitats in the original sample strongly constrain their proportions in the rarefied sample.

We used a stratified bootstrap, where the same numbers of plots were drawn from both the members of the habitat complex pair. Then, the alpha, beta, and gamma diversity were calculated for both halves of the bootstrap sample, which resulted in estimates for natural and managed sites. Finally, the difference between the values in natural and managed sites was calculated in each bootstrap sample. Ten thousand bootstrap samples were drawn for each pair, mean differences were estimated as the mean of the bootstrap values, and the borders of the 95% confidence intervals were estimated by 250th and 9750th values among the ordered bootstrap values

All the analyses were conducted on two sets of species: all species and specialist species. This classification represents the faithfulness (or fidelity) of the species to natural vegetation types (Becking, 1957), in line with the use of the term by Clavel et al. (2011) and Naaf and Wulf (2010). The grouping of the species was based on the social behavior type classification of the Hungarian flora by Borhidi (1995) .

All analyses were done in an R 3.5.3 environment (R Core Team, 2019) using “boot” add-on package (Canty and Ripley, 2017).

3. Results

In the 24 study sites, we recorded 391 relevés, in total, and detected 1180 species. That is 50% of the flora of 93,000 km^2 in Hungary were found in quadrats with an area of only 0.15 km^2 altogether. 49% of the recorded species belonged to the specialist group. In Table A1, we showed the areas of the studied habitat types in the study sites, the number of relevés, as well as the recorded number of all and specialist species.

Table 2. The detected total and specialist species richness of the study areas and the results of statistical analyses based on the bootstrap estimations of the total and specialist species richness distributions.

Habitat complex	Forest-steppe complex on loess				Forest-steppe complex on dolomite				Forest-steppe complex on calcareous sand				Alkaline habitat complex				Freshwater marsh complex				Complex of zonal colline forests			
Site pair	Sárhegy-Gereg		Ostorosvölgy-Novaj		Tés-Várpalota		Csákvár-Zalahaláp		Csévharaszt-Kunadacs		Bócsa-Tázlár		Kelemenszék-Bábaszék		Büdösszék-Sóstó		Bodrogkeresztúr-Pácin		Szabadszállás-Izsák		Felsőtárkány-Bükkzsérc		Diósjenő-Nagybörzsöny	
Code	L1		L2		D1		D2		S1		S2		A1		A2		M1		M2		F1		F2	
Species set	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist	total	specialist
Alpha			*	*	*	*												*						
Beta							*	*											*					
Gamma	*	*		*		*	*	*										*	*	*				

In case of the site pairs, the first one is the name of the natural site, and the second is the managed site. The codes are the same ones used in the map of Fig. 1. We provided separate results for the pools of the total species and the specialist species. Alpha, beta, and gamma show the results of the comparison of the estimated alpha, beta, and gamma diversity measures, respectively, in the natural and managed sites. * denotes that the 95% range of the difference between the estimated species number values did not contain 0 and the value in the natural site was higher. (See also Fig. 2 and Fig. A1 for the difference values.)

We found significant differences in three habitat complexes, namely in the Forest steppe on loess, Forest steppe on dolomite, and Freshwater marsh (Table 2). In these three habitat complexes, the gamma diversities of the specialist species were significantly higher in both the natural sites than in the corresponding managed sites (Fig. 2). In three natural–managed pairs (L2, D1, M1), we found significant differences only in the specialist species, which means that 9 out of the possible 12 gamma diversities proved higher in the natural sites. Regarding alpha and beta diversities, only 8 of the possible 24 differences were significant, and no matching of alpha and beta diversity differences occurred.

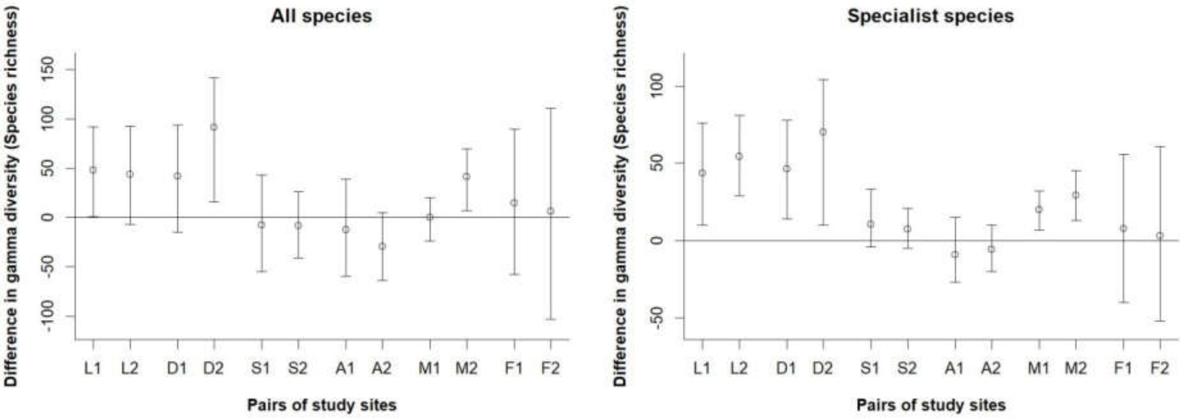

Figure 2.

4. Discussion

In the case of three habitat complexes, namely the forest-steppe on sand, the alkaline habitat complex, and the colline forests, we could not reject the null hypothesis, i.e., the diversity measures for the natural and managed sites were not significantly different. However, in case of the forest-steppe complexes on loess and dolomite as well as the marsh complex, the gamma diversities of the specialist species pool were significantly higher in the natural sites.

The results show that gamma diversity proved to be the most informative variable, and the specialist set of species were more sensitive to the differences between the natural and managed sites than the set of all species. The significant differences in the gamma diversity of the specialist species between natural and managed sites predicted significant differences in the other diversity measures in the same habitat complex. Subsequently, there were no significant differences in the diversities in habitat complexes where specialist gamma diversities were not different. This indicator feature is in agreement with the general finding that the specialist species are particularly sensitive to the degradation processes both globally (Clavel et al., 2011) and also in the case of the grasslands of the forest steppe biome (Deák et al., 2016).

However, we never found both the alpha and beta diversity to be significantly higher in the natural sites, which would automatically lead to significant differences in gamma diversity (Jost, 2007). Thus, the differences between the natural and managed areas were never significant as they would manifest both in the local species richness and dissimilarities between the local assemblages. In two cases (L2 and D1 pairs, all species) we found that the alpha diversities were significantly higher in the natural sites while the gamma diversities were not so. The beta diversities of these pairs were apparently the same (Appendix A, Fig. A1 , upper left), while the gamma diversities were close to be significantly different (Fig. 2, left).

We found 50% of the Hungarian flora (Simon, 2000) in 0.00016% of the area of the country, which means that the observed average species-area curve of the survey (Rosenzweig, 1995) was much steeper than the expected curve for Hungary (Appendix A, Fig. A2). This shows that the sampling strategy we chose proved to be effective in detecting the species richness of the vegetation at the scale of our study. The stratified bootstrap statistical method provided an opportunity to compare the diversity of the pairs of heterogeneous study sites with different habitat compositions.

4.1. Habitat complexes

Although we analyzed the statistics on diversity comparisons for pairs of sites, we discuss the results for the habitat complexes for the two pairs of sites because the plot and site level diversity comparisons showed a consistent pattern: there were either no significant diversity differences in any of the natural–managed pairs, or there were significant differences in the gamma diversities of the specialist species pool in both the natural–managed pairs, which were accompanied by some other significant differences.

4.1.1. Forest-steppe complex on loess

The gamma diversities of the specialist species were significantly higher in the natural sites than the managed ones. The ratios of the scrublands and woodlands were considerably higher in the natural sites (51% vs 18% combined), and one of the woodland types of the natural sites was absent in the managed ones in each pair (Table A1). Moreover, in each pair and in each habitat type, the number of specialist species found was smaller in the managed sites (Table A1). Accordingly, we found a significant alpha diversity decrease in the case of pair L2 (Table 2). A major threat for the forest steppe biome is habitat loss due to the high fertility of the soil at continental scales (Dengler et al., 2014; Werger and van Staalduinen, 2012) and in the Pannonian region (Illyés and Bölöni, 2007; Molnár et al., 2012). The loss of shrublands and woodlands may particularly contribute to the decrease in species richness because of the high diversity of the edge communities (Erdős et al., 2014).

4.1.2. Forest-steppe complex on dolomite

The partly open woodland components of both natural sites were more extended than the managed ones (D1: 87% vs 33% and D2: 87% vs 2%, in natural vs managed sites, respectively, see Table A1) because of the historical land use as pasture, which had reduced the woodland component (Bölöni et al., 2008). Furthermore, the species richness values of specialists were higher in the natural sites for 10 out 12 possible habitat type comparisons (see Table A1), and 7 of the 12 diversity estimations of the natural sites were significantly higher than those of the managed sites. The managed Zalahaláp site consisted almost exclusively of calcareous rock steppes (380 ha out of 394 total area, see types H2 and H3 in Molnár et al., 2008). This resulted in lower beta diversity values because the lack of habitat type diversity was detected due to the bootstrap method applied.

4.1.3. Forest-steppe complex on calcareous sand soil

The woody component of this complex was considerably smaller in the managed sites than in the natural ones (31% vs 3%) but this did not lead to significant differences in the diversity measures because the studied dominant habitat types, the open and closed grasslands, are similarly diverse in the natural and managed sites even in the case of secondary grasslands. The regeneration potential of grasslands is exceptionally high (Csecserits et al., 2011; Ödman et al., 2012; Szitár et al., 2014), so the major problem in preserving the elements of the forest-steppe in sand is the habitat loss in the grasslands (Biró et al., 2008) and the open and closed woodlands (Bölöni et al., 2008; Rédei et al., 2020).

4.1.4. Alkaline habitat complex

The vegetation of the alkaline habitat complex is highly adaptable to extreme environment (Molnár and Borhidi, 2003; Török et al., 2012); therefore, the vegetation type, which comprises highly specialized species, strongly indicates the soil and water features (Tóth and Rajkai, 1994). Most of the human impact is related to changes in the water regime (Ladányi et al., 2016). In fact, the decrease in water table in the Great Hungarian Plain led to the disappearance of many soda pans with their alkali steppe surroundings (Bagi, 1988; Biró et al., 2008). The more moderate human induced degradation forms, such as overgrazing or trampling, are hardly indicated by the highly specialized flora (Tóth and Kertész, 1993). Although our natural and managed sites were distinguished by the field botanists of the MÉTA habitat mapping project (Molnár et al., 2008), we could not find clear differences either in habitat type composition or in vegetation diversity.

4.1.5. Freshwater marsh complex

In the case of both pairs of the freshwater marsh complexes, we detected significantly higher gamma diversities for the specialist species of the natural sites than the managed ones. The differences in habitat type compositions and slightly larger specialist species pool of the natural sites explain this result. The only woodland habitat, the willow mires and shrublands, covered considerably larger areas in the natural sites (M1 – 29% vs 3% and M2 – 20% vs 0% in natural vs managed sites, respectively. See Table A1), which is similar to most of the water-logged habitats dominated by *Phragmites, Phalaris, Glyceria,* and *Schoenoplectus* (M1 – 36% vs. 20% and M2 – 32% vs 10%). On the contrary, the managed sites were mostly covered by different types of meadows, including oversown stands (M1 – 25% vs 71% and M2 – 35% vs 77%). Besides the difference in habitat composition, the recorded numbers of specialist species were higher in the natural sites in 10 out of 14 habitat type comparisons. We concluded that the reason for the significantly higher specialist gamma diversity values in the natural sites was the reduced landscape heterogeneity of the managed sites due to lower water table level and more intensive land use (Biró et al., 2008; Csaba et al., 2015; Shi et al., 2010).

4.1.6. Complex of zonal colline forests

We did not find any significant differences in the species diversities of the natural and managed sites in the colline forest complex. This shows that the architecture, species composition, and age distribution of the canopy, which were the criteria for naturalness determination in the MÉTA habitat mapping project (Bölöni et al., 2008), do not necessarily distinguish between the diverse and less diverse understory, which determines the species diversity. Moreover, even the "natural" sites did not consist of primeval or truly old-growth stands with a natural fauna and disturbance regime, including gap dynamics, because there are not enough old-growth forests in Hungary for a study at a 2 x 2 km scale (Paillet et al., 2010). The relatively well managed stands (i.e., without a long deforested stage, erosion, or plantation) showed the same diversity, which is in agreement with other studies (Bartha et al., 2006; Lindenmayer et al., 2006; Standovár et al., 2006).

5. Conclusion

We found, corresponding to our expectations, that the most sensitive variable of the diversity to land use was the gamma diversity of the specialist species pool. We also found that the diversity values were higher in the natural sites of the forest steppe complex on loess, forest steppe complex of dolomite, and freshwater marshland complex. The common feature of these natural–managed pairs was that the woody component was considerably lower on the managed sites, which made them less heterogeneous at the landscape scale. In the case of the freshwater marshland complex, the habitats with the highest water levels were also lower, further decreasing the landscape heterogeneity. On the contrary, in the case of the other three complexes, the natural and the managed sites were similarly heterogeneous. The high disturbance tolerance and regeneration capacity of the sand vegetation and the highly specialized stress tolerant vegetation in the alkali habitat complex made the moderate intensity human land use virtually undetectable by means of species diversity.

We concluded that the same differences in naturalness may represent the different sensitivities of the habitat complexes to human management, which are characterized by differences in diversity measures. We identified three more sensitive habitat complexes, the loess and dolomite forest steppe and the freshwater marshland. In these complexes, special attention would be required for preserving the most vulnerable habitat types (Biró et al., 2018; Hoekstra et al., 2005), the woodlands and the water-logged habitats. In the case of the other three complexes, the moderate human land use can be harmonized with nature protection goals (Hannah et al., 1995).

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Figure 1. Map of study sites. Empty circles denote natural sites and filled ones denote managed sites. See the names of the sites in Table 2.

Figure 2. The 95% confidence intervals of the differences in gamma diversity estimations between the natural and managed sites using bootstrap method.
Diversity was measured by species richness. The codes are the same ones used in Table 1 and Fig. 1. Positive values denote higher diversity in the natural sites. Significant differences were found where the whiskers did not cross the 0 line.

List of tables

Table 1. Six characteristic habitat complexes that represent a majority of the natural habitats in Hungary.

Table 2. The detected total and specialist species richness of the study areas and a summary of the results of the statistical analyses based on bootstrap estimations of the total and specialist species richness distributions.

In case of the site pairs, the first one is the name of the natural site and the second is the managed site. The codes are the same ones used in the map of Fig. 1.We provided separate results for the pools of the total species and the specialist species. Alpha, Beta, and Gamma show the results of the comparison of the estimated alpha, beta, and gamma diversity measures, respectively, of the natural and managed sites. * denotes that the 95% range of the difference between the estimated species number values does not contain 0 and the value in the managed site was higher (See also Fig. 2 and Fig. A1 for the difference values).

Appendices

Appendix A

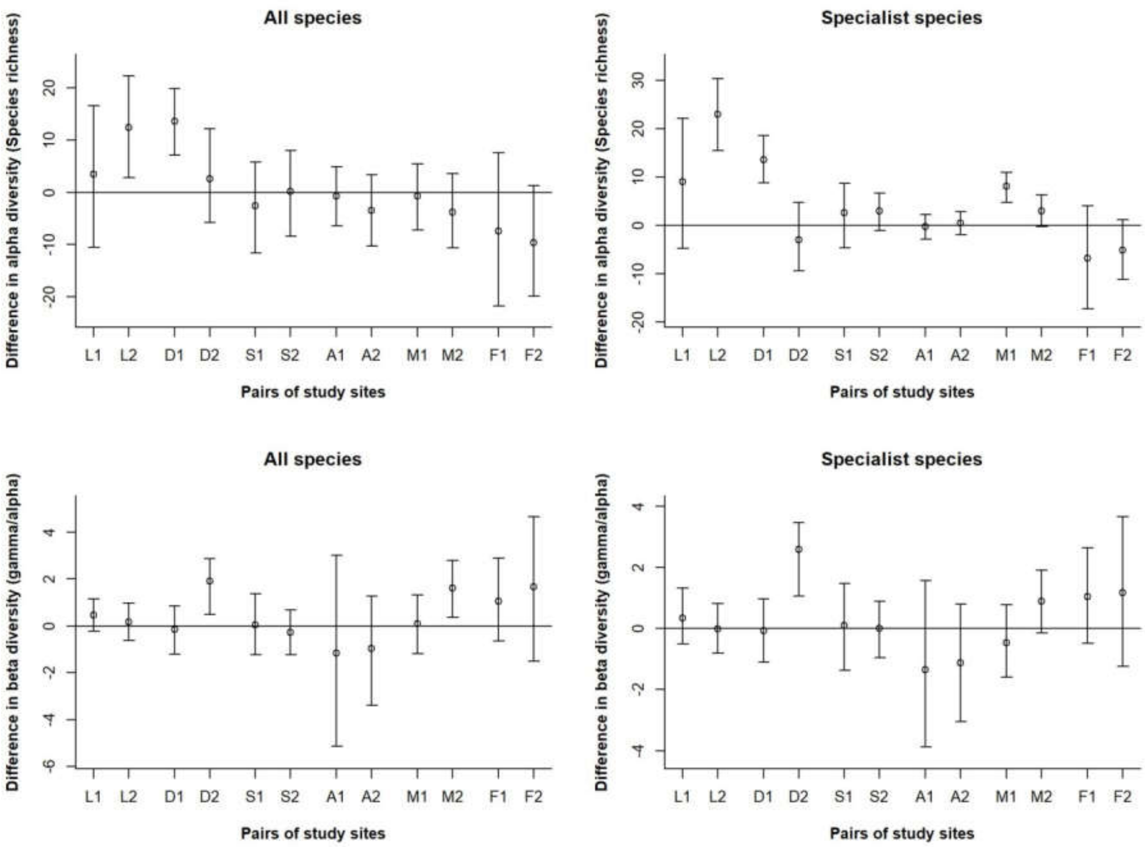

Figure A1. The 95% confidence intervals of the differences in alpha diversity (above) and beta diversity (below) estimations between the natural and managed sites using bootstrap method. Alpha diversity was measured by species richness; the "gamma/alpha" measure for beta diversity is the theoretical number for habitat types with no common species. The codes are the same ones used in Table 2 and Fig. 2. Positive values denote a higher diversity in natural sites. Significant differences were found where the whiskers did not cross the 0 line.

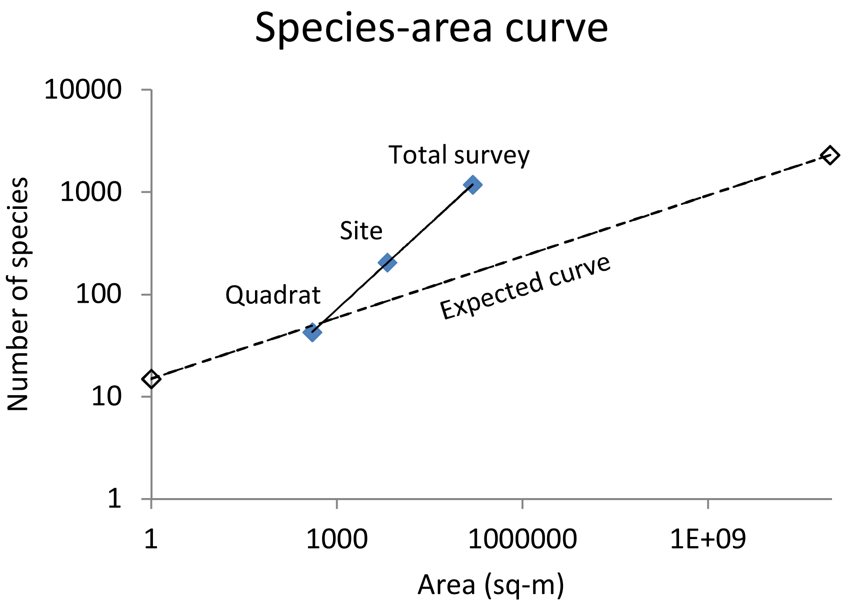

Figure A2. Average vascular plant species-area curve of the survey with the expected species-area curve for Hungary. Quadrat – average species number of 42.6 in a 400 m^2 sampling unit; site – weighted average species number of 205.7 in a weighted average sampled area of 6517 m^2, which is weighted by the number of quadrats per sites; survey – total recorded species number of 1180 in a total sampled area of 156400 m^2; expected curve – the endpoints are 15 species in 1 m^2 (educated guess) and 2300 species in 93000 km^2.

Table A1. The investigated areas of the study sites, the number of relevés, the detected species numbers and specialist species numbers, and their breakdowns by habitat types.
See the names of the study sites in Table 2 of the main text. Note that the total species numbers are not the sum of the species numbers by habitat types.

		Area (ha)				No. of plots				No. of species				No. of specialist species			
	Pairs	Pair 1		Pair 2		Pair 1		Pair 2		Pair 1		Pair 2		Pair 1		Pair 2	
Habitat complex	State	natural	managed	natural	managed	natural	managed	natural	managed	natural	managed	natural	managed	natural	managed	natural	managed
Forest-steppe complex on loess	Steppe shrublands	95	42			3	3			145	146			76	67		
	Forest-steppe meadows	49	13	69	59	3	3	3	3	150	173	142	113	115	108	95	55
	Steppe oak woodlands	12	16	77		3	3	3		151	133	151		112	69	100	
	Semi-dry grasslands	1	19	35	24	3	3	3	3	142	143	128	134	104	73	72	59
	Steppic rock grasslands	73	38	1	130	3	3	2	3	171	138	106	109	100	78	62	47
	Closed oak woodlands	40		9	3	2		3	2	109		84	66	69		56	32
	Total	270	128	191	216	17	15	14	11	356	293	280	236	214	159	169	107
Forest-steppe complex on dolomite	Mesic deciduous woodlands	215	41	4		3	3	3		107	75	63		87	55	43	
	Forest-steppe meadows	9	60	6	4	3	3	3	3	110	84	119	109	72	48	69	47
	Dawny oak woodlands	41	68	277	1	3	3	3	3	107	73	71	120	77	46	43	67
	Calcareous rock steppes	37	194	38	380	3	3	3	3	67	76	80	67	56	53	65	46
	Scrub and rock woodlands	63	14	41	5	3	3	3	3	128	149	139	113	75	81	107	49
	Closed rock grasslands	1	1	1	4	3	3	2	3	96	110	81	82	81	78	70	62
	Total	366	378	367	394	18	18	17	15	290	270	269	241	201	172	186	133
Forest-steppe complex on calcareous sand	Open secondary sand grasslands	13	4		39	1	2		2	39	62		58	18	12		17
	Closed secondary sand grasslands	8	17		9	2	1		1	74	55		62	22	6		12
	Poplar-juniper steppe woodlands	41		109	21	3		3	3	72		71	57	42		34	26
	Closed oak woodlands	18				3				40				13			
	Open sand steppes	36	133	191	172	3	3	3	3	52	51	46	47	30	20	26	22
	Open oak woodlands	3				3				63				27			
	Closed sand steppes	19	129	54	45	3	3	3	3	66	91	66	82	42	48	37	34
	Sand steppe poplar woodlands	18	43	35	31	3	3	2	3	78	61	44	45	36	12	15	10
	Total	156	326	389	317	21	12	11	15	195	187	125	145	85	62	56	48
Alkaline habitat complex	Alkaline meadows	7	29	95	33	3	2	2	3	17	11	13	55	10	9	8	28
	Reed beds	3	17	7	3	3	3	1	3	2	8	4	23	1	6	2	11
	Puccinellia swards	107		32	77	3		1	3	17		18	9	15		10	7
	Closed steppes	18	31	41	44	3	3	3	3	77	66	49	56	25	30	20	13
	Achillea and artemisia alkaline steppe		46	51			3	3			13	25			11	19	
	Annual alkaline pioneer swards	101	82	2	1	3	3	3	1	9	5	15	4	8	5	11	3
	Bolboschoenus beds	80	57	139	37	3	3	2	3	6	12	9	17	4	10	6	11
	Total	316	262	367	195	18	17	15	16	95	83	76	116	40	45	40	50
Freshwater marsh complex	Willow mires and shrublands	107	10	76		3	2	3		39	42	60		27	17	44	
	Deschampsia meadows			18	23			3	3			64	74			46	43
	Alopecurus meadows	92	221			3	3			40	45			28	14		
	Oversown meadows		2		41		1		3		35		70		10		31
	Glyceria beds	20				3				39				33			
	Tall sedge beds	34	18	7	39	2	3	3	3	26	43	54	45	22	26	44	37
	Reed beds (incl. Phalaris)	47	63	124	33	2	3	3	3	35	23	34	37	27	13	27	27
	Mesotrophic meadows			115	203			3	3			83	80			46	39
	Semi-dry grasslands			45	8			3	3			66	59			27	21
	Scheonoplectus beds	65				3				19				18			
	Total	365	314	385	347	16	12	18	18	80	110	196	156	58	46	112	87
Complex of zonal colline forests	Beech woodlands	52		116	97	1		3	3	20		53	69	19		37	49
	Turkey oak - sessile oak woodlands	93	261		10	3	3		1	115	109		51	81	83		31
	Riverine ash-adler woodlands	2	1			2	1			79	67			59	47		
	Spring wetlands			1	1			1	2			40	66			30	41
	Oak-hornbeam woodlands	68	102		115	3	3		1	73	82		47	57	63		31
	Acid oak woodlands	15	4	25		3	3	1		94	109	52		71	73	34	
	Termophilous oak woodlands and scrub	14	6		24	3	3		2	49	84		75	37	69		55
	Colline meadows	10	6	12	1	1	1	3	1	59	76	160	79	29	43	92	36
	Rock grasslands				5				1				83				34
	Beech stands with no understory	79		174	145	3		3	3	20		27	25	15		23	19
	Acid beech woodlands			17	3			3	3			23	64			19	49
	Ravine woodlands	11	20	5	1	2	1	2	1	70	10	46	38	51	10	31	22
	Rocky slope woodlands	40		8	1	2		3	2	52		117	89	31		72	56
	Total	384	400	358	400	23	15	19	20	247	250	285	271	172	176	179	163

Appendix B

The dataset of vascular plant relevés used in the manuscript.

391 relevés from 24 sites, arranged in 12 Excel sheets; each consists of a natural-managed site pair.

File – Different impacts – Appendix B.xlsx