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The Influence of Forest/Grassland Proportion on the Species Composition, Diversity and Natural Values of an Eastern Austrian Forest-steppe[1]

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Abstract—Eastern Austrian forest-steppe remnants are extremey important both from conservation and a scientific perspective, yet case studies integrating the examination of the grassland and the forest components are relatively scarce. Consequently, the knowledge on how the pattern of forested vs. non-forested patches influences species composition and diversity remains rather limited. In this study, we compared three sites with different forest/grassland proportions: grassland with a low canopy cover, a mosaic area with alternating forest and grassland habitats, and a forest with some canopy gaps. Our aim was to find out which one of them is the best for conservation purposes. We found that the grassland and the mosaic area had a similar composition, while the forested one was distinct from them. The mosaic vegetation seemed to be the most species rich, also hosting a high number of red-listed species. Beside forest-related and grassland-related species, the mosaic plot also supported some edge-related plants. We conclude that the preservation of mosaic-like forest-grassland habitats is the most favorable for conservation aims. Nevertheless, several species, among them some red-listed ones, were clearly linked either to the forest or to the grassland plot. Therefore, even though mosaics deserve a special attention, open grasslands and xeric forests should also be preserved.

Keywords: habitat heterogeneity, spatial pattern, xeric communities, conservation

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Forest-steppes form a separate vegetation belt, ranging from eastern Europe to the easternmost parts of Asia [1]. This zone forms a transition between the closed forests and the steppes, and can be characterized by intermittent grassland and forest patches. Despite its extremely high conservation value, the forest-steppe belt is among the most threatened biomes on Earth [2]. Consequently, there is an increasing need for studies that may contribute to an improved preservation of these habitats.

E.M. Lavrenko [3] divided the forest-steppes into five large geobotanical units. The group of European oak forest-steppes may further be subdivided into a continental and a submediterranean type [4, 5]. Eastern Austrian forest-steppes should be classified into this latter type.

Forest-steppes are among the most unique and most threatened habitats in eastern Austria [6, 7], thus their conservation is of primary importance. In addition, they have a significant biogeographic importance, since they represent the westernmost zonal Eurasian forest-steppes [1, 8–11], besides some small and isolated remnants in the inner-alpine dry valleys and Germany [11]. Because of their marginal position, Austrian forest-steppes should be regarded as particularly vulnerable communities to environmental changes [12]. Unfortunately, considerable uncertainties exists regarding (1) their "natural" spatial pattern (i.e. prior to intensive human impact) and (2) the most desirable pattern of grassland and forest patches. The first topic includes questions such as the role of native ungulates, fire events, climate and edaphic parameters in maintaining treeless patches and enabling the existence of a mosaic pattern [13–17]. Concerning the second topic (which is, of course, not independent of the first one), the following questions may emerge: Which grassland vs. forest proportion is optimal for the overall diversity and for particular species? Should conservation activity counteract successional processes and maintain grasslands? Do variously sized

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forest and grassland patchess have different conservation values?

The majority of the earlier studies focused either on the xeric forests or the dry grasslands of the region [14, 18–20], without considering the inter-relationships between these landscape components. This isolated focus on individual components seems to be unsatisfactory for an in-depth understanding of forest-steppe characteristics. Forest-steppes are composed of differently sized forest patches and grassland patches, plus the forest edges between them [21, 22]. The exact role of these components in maintaining species diversity and supporting species of high conservation value is not fully understood. Although the grassland component is usually considered to be a more threatened habitat (due to successional processes following the abandonment of grazing), it has been shown for the Pannonian biogeographical region that the forest patches and their edges also have an extremely high importance in maintaining diversity on the landscape level [23–25].

As habitat restoration projects and active conservation management activities are being carried out to protect and maintain forest-steppe habitats, the need for more information on the optimal patterns becomes increasingly important. The aim of this study was to contribute to a better understanding of how the spatial pattern of forested and non-forested patches influences the species composition and diversity of the forest-steppes. We compared three sites with different forest/grassland proportions, and examined which arrangement is the best for conservation purposes.

MATERIAL AND METHODS

Study Area

Our study area was located on the southeastern slopes of Glaslauterriegel Hill (N 48°2′8″, E 16°15′26″, part of the Anninger Mts) situated between the settlements Pfaffstätten and Gumpoldskirchen. Bedrock is limestone, soil is rendzina. Mean annual temperature is 9.9°C, mean annual precipitation is 615 mm [26]. The study area belongs to the Natura 2000 network (protected area Nr. 11, Wienerwald-Thermenregion).

Traditional land-use of the xeric vegetation mosaic was grazing; it was abandoned temporarily but has been restored recently.

In the forest component, which can be classified into the association *Geranio sanguinei-Quercetum pubescentis* [27], canopy cover varies from very open (20%) to relatively close (80%), and the dominant species is *Quercus pubescens*. In the shrub layer, *Cornus mas* is by far the most frequent and abundant species. Herb layer cover has a wide range, from almost bare patches to 70%. Typical species include *Brachypodium sylvaticum*, *Carex michelii*, *Geum urbanum*, *Laserpitium latifolium*, *Polygonatum odoratum*, and young individuals of trees and shrubs. *Convallaria majalis* can reach high cover values locally.

In the grassland component, belonging to the association *Scorzonero austriacae-Caricetum humilis* [19, 20], vegetation cover usualy varies between 50 and 80%. Main species are *Brachypodium pinnatum*, *Bromus erectus*, *Cervaria rivini*, *Festuca valesiaca*, *F. rupicola*, *Koeleria macrantha*, *Melampyrum cristatum*, *M. nemorosum*, *Polygonatum odoratum* and *Stipa pennata*.

Field Works

In the study site, three 20 m × 30 m plots were selected ("large plots") with different forest/grassland proportions. In the first large plot (henceforth the "grassland plot"), canopy cover was only 7%. The area is grazed by sheep at least every second year (N. Sauberer personal communication). The second large plot (henceforth the "mosaic plot") represents a nearly equal forest/grassland proportion, with a canopy cover of 45%. It is a typical savanna-like pattern characteristic of temperate forest-steppes. The area had only a few trees in the 1960s, but tree cover has increased considerably since then [28]. Currently it is grazed by sheep each year (N. Sauberer personal communication). The third large plot (henceforth the "forest plot") had a canopy cover of ca. 75%, forming a xeric forest with canopy gaps and openings. The canopy layer of the area was much more open in the 1960s [28]. Grazing presumably ended here in the 1940s or 1950s; there is no active management here at present (N. Sauberer, personal communication). All of the large plots were situated within the elevation range 310–335 m, with the same exposition and similar slope inclination values.

Within each large plot, twenty 2 m × 2 m plots were established ("small plots") in a regular arrangement in a grid. We had a total of 60 small plots (3 canopy cover grades × 20 replicates). Coenological relevés were prepared in June 2015, by visually estimating the percentage cover of all vascular plant species of the herb layer.

Plant species names follow [29].

Data Analyses

A DCA-ordination (detrended correspondence analysis, [30]) was performed to study the coenological similarity of the 60 relevés. We chose this ordination technique because it is able to eliminate the arch-effect, which is expected for data with a gradient-like character (in this case extending form relatively open to more closed sites). The ordination was based on the logarithms of species' cover values, rare species were downweighted. For the analysis, we used the software CANOCO 5.0 [31, 32].

To gain more detailed information on the similarity of the large plots' species pools, we prepared area-proportional Venn-diagrams, using BioVenn, an on-line

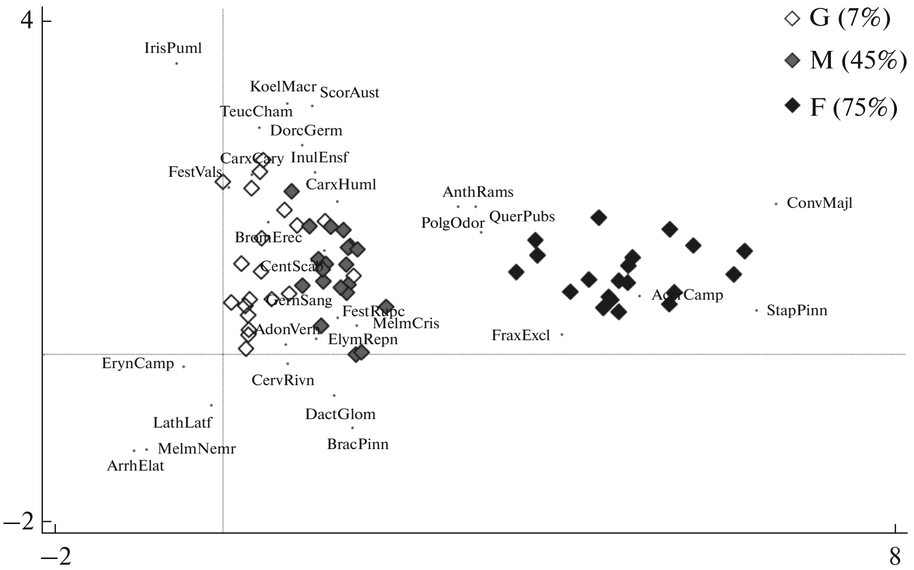

Fig. 1. DCA ordination biplot of the 60 2 m × 2 m relevés and the most important 30 species. Relevés were made in the large plots as follows: G = grassland plot, M = mosaic plot, F = forest plot. Canopy cover of the large plots is given in parentheses. Percentage variances explained by the first and second DCA axes were 15.76 and 4.57%, respectively. AcerCamp = *Acer campestre*, AdonVern = *Adonis vernalis*, AnthRams = *Anthericum ramosum*, ArrhElat = *Arrhenatherum elatius*, BracPinn = *Brachypodium pinnatum*, BromErec = *Bromus erectus*, CarxCary = *Carex caryophyllea*, CarxHuml = *Carex humilis*, CentScab = *Centaurea scabiosa*, CervRivn = *Cervaria rivini*, ConvMajl = *Convallaria majalis*, DactGlom = *Dactylis glomerata*, DorcGerm = *Dorycnium germanicum*, ElymRepn = *Elymus repens*, ErynCamp = *Eryngium campestre*, FestRupc = *Festuca rupicola*, FestVals = *Festuca valesiaca*, FraxExcl = *Fraxinus excelsior*, GernSang = *Geranium sanguineum*, InulEnsf = *Inula ensifolia*, IrisPuml = *Iris pumila*, KoelMacr = *Koeleria macrantha*, LathLatf = *Lathyrus latifolius*, MelmCris = *Melampyrum cristatum*, MelmNemr = *Melampyrum nemorosum*, PolgOdor = *Polygonatum odoratum*, QuerPubs = *Quercus pubescens*, ScorAust = *Scorzonera austriaca*, TeucCham = *Teucrium chamaedrys*, StapPinn = *Staphylea pinnata*.

Venn-diagram generator tool (http://www.biovenn.nl/). A second Venn-diagram was also made, taking into account only the red-listed species of the large plots. Species' categorization as red-listed followed [33].

In order to identify species that are associated to a certain level of canopy cover, we calculated the phi coefficient, which is one of the most reliable measures of fidelity [34]. Species with high phi values preferably occur within a given large plot (with a certain canopy cover value), while avoid different canopy closure. Analyses were carried out with JUICE 7.0 [35]. Non-significant diagnostic species were excluded with Fisher's exact test.

We calculated species number and Shannon diversity for each small plot, using Past 3.06 [36]. Data were tested for normality with the Shapiro-Wilk test. Per plot species number and Shannon diversity were compared between the different canopy cover values of the large plots, using One-way ANOVA and subsequent Tukey's pairwise comparisons. Statistical analyses were done with the program package SPSS 22.0 (SPSS Inc).

Since the selection of diversity indices (such as the Shannon diversity) is always arbitrary and thus can be criticized, we also used diversity ordering as a possible solution to this problem. Rather than selecting one or a few diversity indices, diversity ordering allows the comparison of the large plots according to several diversity functions [37]. In this study, we used Rényi's one parameter diversity index family, which results in a series of different diversity indices when the scale parameter α is increased. In the graphical output, diversity values of the three large plots are plotted against the scale parameter, resulting in one profile for each large plot. If the profile of one large plot is above the profile of the other ones, this means that this plot is the most diverse, according to all indices analyzed.

RESULTS

The DCA-ordination (Fig. 1) indicated that the gradient was rather long (gradient length: 6.2), suggesting a complete species turnover between the relevés with low and high canopy cover values. The relevés from the grassland, the mosaic and the forest plots (i.e. low, intermediate and high canopy covers in the large plots) were clearly separated along the first axis, although the relevés from the grassland and the mosaic plots were close to one another in the ordination space, forming two slightly overlapping groups.

According to the Venn-diagram (Fig. 2), it can be seen that the forest plot was quite species-poor, compared to the other two large plots. In addition, this large plot was the most distinct: although overlaps did

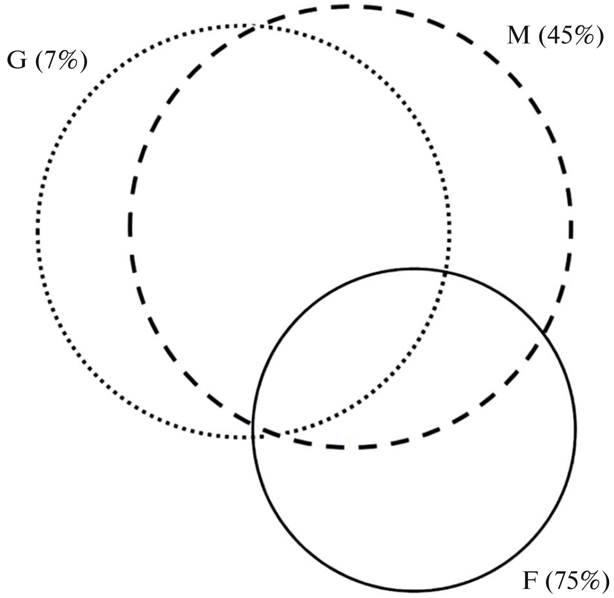

Fig. 2. Area-proportional Venn-diagram of the three large plots (G = grassland plot, M = mosaic plot, F = forest plot, canopy covers in parentheses), based on all species found in the plots.

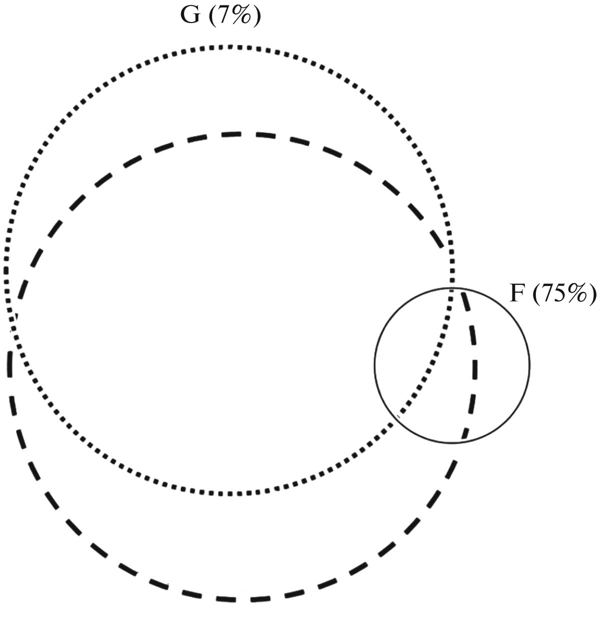

Fig. 3. Area-proportional Venn-diagram of the red-listed species of the three large plots (G = grassland plot, M = mosaic plot, F = forest plot, canopy covers in parentheses).

exist, the number of species restricted to this plot was high. The grassland and the forest plots were the most distinct from each other regarding their species pool. In contrast, the grassland and the mosaic plots were similar, with a large overlapping area.

The picture was rather different if only the red-listed plant species were considered. The grassland and the mosaic plots had roughly the same amount of red-listed species, while the forest plot proved to be especially poor in red-listed plants (Fig. 3).

The number of significant ($p < 0.001$) diagnostic species was as follows: grassland plot 9, mosaic plot 14, forest plot 12 species (table). The grassland plot had several grassland-related plants among the diagnostic species (e.g. *Bromus erectus* and *Festuca valesiaca*). In the mosaic plot, some diagnostic species are known to prefer edges (e.g. *Cervaria rivini* and *Geranium sanguineum*). Among the diagnostic species of the forest plot, there were many trees and shrubs (e.g. *Acer campestre* and *Euonymus europaeus*), and also some forest-related herbs (e.g. *Alliaria petiolata* and *Geum urbanum*).

According to the One-way ANOVA, species number differed significantly among the three large plots ($F = 54.66$, $p < 0.001$). Tukey's pairwise comparisons indicated that the forest plot hosted significantly fewer species than the grassland plot ($p < 0.001$) or the mosaic plot ($p < 0.001$). Although the mosaic plot seemed to possess the highest species number per small plots, the difference was not significant ($p = 0.081$), when compared to the grassland plot (Fig. 4a).

Shannon-diversity also differed significantly among the large plots (ANOVA: $F = 3.9$, $p < 0.026$). According to Tukey's pairwise comparisons, the diversity of the grassland plot was significantly smaller than the diversity of the mosaic plot ($p = 0.032$). Differences were not significant for the other comparisons (Fig. 4b).

The diversity ordering clearly indicated that intermediate canopy cover (in the mosaic plot) enables the largest diversity in the entire range of the scale parameter (i.e. according to several diversity indices) (Fig. 5). The case was more complicated for the other two canopy cover values. Towards the left end of the graph, the grassland plot was more diverse than the forest plot, while the opposite was true towards the right end of the graph, thus the two large plots with intersecting profiles could not be ordered according to their diversities.

DISCUSSION

Mixed forest-grassland ecosystems are currently in the focus of ecological interest worldwide [38, 39]. The forest-steppes of eastern Austria have an outstanding theoretical and practical importance, being the westernmost forerunners of the Eurasian forest-steppe zone, and providing habitats for a large number of endangered species. This study aimed to analyze the influence of different canopy cover values on species composition and diversity, and to provide information on the spatial pattern that is most beneficial from a nature conservation point of view.

There are different explanations regarding the "natural" spatial pattern of forest and grassland patches in forest-steppe areas. Although the western parts of the steppe and forest-steppe zones contain a lot of remnant species from the Pleistocene steppes, the flora has been enriched with submediterranean species and trees in postglacial warmer periods [40]. Even the influence of natural ungulates on the vegetation of these sites in the warm and humid Atlantic period – also the arrival of the Neolithic settlers – is controversial [41, 42]. It is presumed that, at least in central Europe, the forest-steppe areas hosted the first settlements of Neolithic cultures [17]. It is possible that the start of early animal husbandry needed forests with openings and gaps, and avoided totally dense and closed forests; thus, the position of Neolithic settlements may correspond to forest-steppe areas [43]. It seems sure that forest-steppes show a continuous human presence for more than 8000 years. Under current climatic conditions, however, they will change to more closed forest types in the absence of grazing, browsing or other historical anthropogenic use (for example coppice with standards, [44], see also [15]).

According to the DCA-ordination (Fig. 1) and the Venn-diagrams (Figs. 2 and 3), the species composition of the forest plot is the most distinct, while the compositional characteristics of the grassland and the mosaic plots are rather similar to each other. This indicates that a mosaic pattern with scattered trees enables the survival of many grassland-related species. Although differences clearly exist between the grassland and the mosaic plots, for most species, 45% canopy cover seems to be well under a certain threshold value, above which grassland-related species disappear and forest-related ones appear.

Diagnostic species of the different canopy covers reflect the habitat characteristics (table). It is particularly conspicuous that the mosaic plot hosts several plants that are usually considered edge-species, for example *Cervaria rivini*, *Geranium sanguineum* and *Melampyrum cristatum* [6, 13, 45]. In addition, *Festuca rupicola* should also be mentioned here. Although it is not exclusively an edge-related species, it has been shown that it significantly prefers edges if environmental conditions are too harsh in the grasslands [24].

Generally, it seems that the mosaic plot is the most beneficial habitat concerning species number and diversity (Figs. 4 and 5). In contrast, the forest plot proved to be the poorest in species, which is particularly obvious for the red-listed species (Fig. 3).

Our results indicate that the highest diversity was linked to the mosaic plot, i.e. to intermediate canopy cover. The most likely explanation for this is that grassland-related species can co-occur here with forest-related ones (although this latter type is clearly under-represented). In addition, edge-related species further contribute to an increased diversity. Thus, among the three patterns studied, the mosaic plot

Phi values of the significant ($p < 0.001$) diagnostic species of the three large plots

	Canopy cover		
	7%	45%	75%
Arrhenatherum elatius	0.612		
Melampyrum nemorosum	0.607		
Festuca valesiaca	0.598		
Bromus erectus	0.593		
Sanguisorba minor	0.558		
Achillea collina	0.526		
Securigera varia	0.484		
Silene noctiflora	0.481		
Stachys recta	0.452		
Anthericum ramosum		0.647	
Melampyrum cristatum		0.637	
Festuca rupicola		0.607	
Inula ensifolia		0.592	
Polygonatum odoratum		0.540	
Aster linosyris		0.535	
Dorycnium germanicum		0.535	
Geranium sanguineum		0.534	
Carex humilis		0.526	
Centaurea scabiosa		0.501	
Helianthemum ovatum		0.484	
Cervaria rivini		0.478	
Scorzonera austriaca		0.469	
Chamaecytisus ratisbonensis		0.452	
Acer campestre			0.858
Fraxinus excelsior			0.761
Euonymus europaeus			0.726
Prunus avium			0.726
Viola sp.			0.721
Staphylea pinnata			0.612
Brachypodium sylvaticum			0.574
Cornus mas			0.574
Melittis melissophyllum			0.574
Alliaria petiolata			0.535
Geum urbanum			0.524
Euonymus verrucosus			0.481

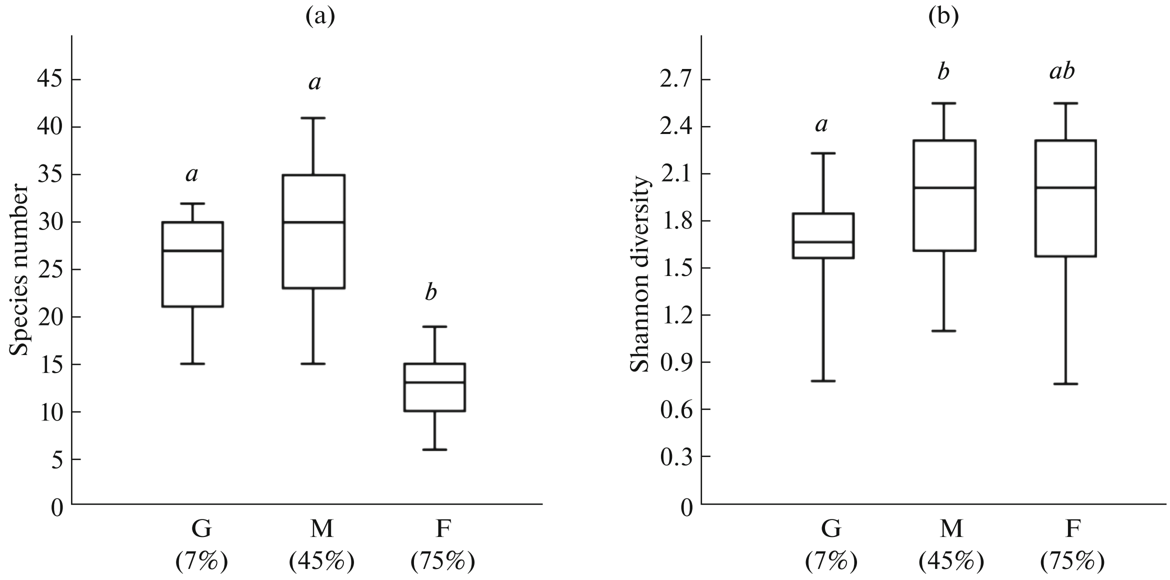

Fig. 4. Species number (a) and Shannon diversity (b) per small plots according to the different canopy cover values of the large plots. G = grassland plot, M = mosaic plot, F = forest plot, canopy covers in parentheses. Boxes not sharing a letter are significantly different.

proved to be the most desirable from a conservation perspective. This result fits in with the well-known fact that spatial and temporal heterogeneity tend to increase diversity [46–48]. It has been observed in several mosaic ecosystems that, regarding species composition, there are considerable differences between the forest and the grassland components. This proved to be the case in Africa [49], America [50], and Europe [21]. The probable causes for this are diverse [51], but it is certain that the high diversity of natural mosaics such as savannas and forest-steppes results from the habitat heterogeneity. That is why mosaics often host a higher diversity than nearby closed forests or open grasslands. For example, in a midwestern oak savanna, Leach and Givnish [52] found that patchy areas were more diverse than either open grasslands or closed forests. Similarly, the results of Peterson and Reich [53] indicated that species richness in a Minnesota savanna was highest under intermediate tree canopy covers, whereas both grassland and forest plots had fewer species.

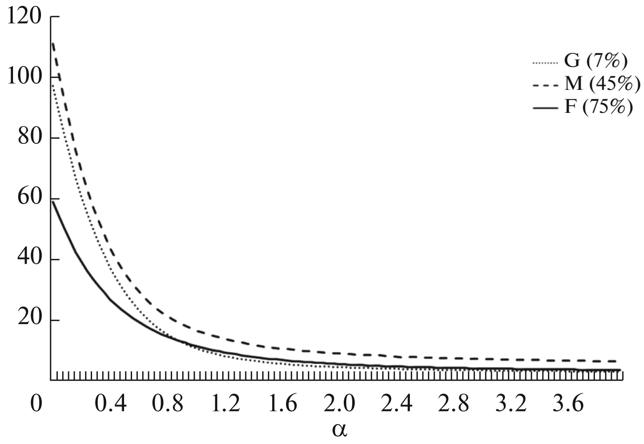

Fig. 5. Diversity ordering of the three large plots. G = grassland plot, M = mosaic plot, F = forest plot (canopy covers are in parentheses).

Quite naturally, the above findings have serious implications for conservation. In forest-steppes, every effort should be made to protect not only the grassland component, but also the forest patches, in accordance with some other recent findings [25, 54].

However, it is important to note that patchiness exists at several spatial scales. At a larger scale, mosaic areas, closed forests and open grasslands themselves form a larger mosaic. It seems likely that all of the components have an important role in these complex ecosystems. In our study, we found several species (including red-listed ones) whose survival was linked either to the forest or to the grassland plot (Figs. 2 and 3, table). If only the mosaics are preserved, all of these species will suffer great losses. Similar patterns occur in different regions. For example, in the South American Cerrado, fine-scale mosaics (consisting of trees, shrubs and grasslands) co-occur with large treeless areas and closed forests, all of which are part of a mosaic at a coarser scale. It has been shown that some species rely on the closed forests or the open grasslands, thus all of the components are necessary to protect the extremely high diversity of the region [55, 56].

To sum it up, in the studied Austrian forest-steppe, grasslands, forested areas and mosaics should also be preserved for conservation purposes. These form a mosaic of higher order, representing a spatial arrangement that supports a high diversity and ensures the survival of several species.

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