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**The effects of different canopy covers on the herb layer in the forest-steppes of the
Grazer Bergland (eastern Alps, Austria)**

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ABSTRACT

The submontane belt of the eastern Alps is dominated by beech forests. However, on rocky and steep south-facing slopes, small vegetation mosaics have developed, which, to a certain degree, are similar to the Pannonian forest-steppes. In spite of their unique conservation importance and threatened status, they have received relatively little scientific attention. In this study we analyzed the spatial pattern of such mosaics. More specifically, our objective was to find out how canopy cover value influences the species composition of the herb layer. According to our results, canopy cover of *Pinus sylvestris* has a rather limited effect on the herb layer composition and species richness. Thus, in the studied canopy cover range (ca. 5–75% canopy cover), most species

occurred under all canopy cover grades. This is presumably a result of the canopy characteristics and branching pattern of *P. sylvestris*: it can be assumed that the physical conditions of the canopy and intercanopy patches are somewhat similar. This is in sharp contrast with the Pannonian forest-steppes dominated by *Quercus pubescens*. We conclude that, even though the cessation of traditional land-use may not result in a rapid change of the composition in eastern Austrian forest-steppes, every effort must be made to conserve these valuable habitats.

KEY WORDS: Styria, forest-grassland ecosystem, mosaic vegetation, spatial heterogeneity, pattern

INTRODUCTION

Eurasian forest-steppes form a transitional belt between the closed forests and the open grasslands, extending from eastern-central Europe almost to the Pacific coast (Walter, Breckle, 2002; Magyari et al., 2010). While continental forest-steppes in Asia and eastern Europe are characterized by a coarse-scale mosaic of alternating large forest patches and large grasslands, submediterranean forest-steppes of eastern-central Europe form a fine-scale mosaic with small vegetation patches (Wendelberger, 1989; Zólyomi, Fekete, 1994; Tölgyesi, Körmöczi, 2012). Situated in eastern-central Europe, the Pannonian biogeographical region is usually regarded as hosting the westernmost forest-steppes (e.g. Borhidi, 2002; Fekete et al. 2002). It is well-known that the northeastern parts of Austria show remarkable similarities towards the Pannonian vegetation. Consequently, forerunners of the forest-steppes can be found even here, which have been studied intensively (e.g. Niklfeld, 1964; Eijsink et al., 1978; Sauberer, Bieringer, 2001; Willner et al., 2013a, b). However, other forest-steppe like habitats have received little attention in Austria.

The eastern parts of the Alps in the Austrian federal state Styria, including the Grazer Bergland (Mountain Region around Graz) are considerably affected by climatic and vegetation influences from eastern and southern directions. For example, *Quercus pubescens*, a thermophilous tree species, has unique occurrences here (Eggler, 1941,

1951; Heber, 2005), constituting a community with several other thermophilous plants. In addition, the proportion of mediterranean and sub-mediterranean plants is relatively high in the area around Graz, although most of these species are restricted to anthropogenic habitats (Eggler, 1934). It is generally accepted that, without human interference, most of the Alps below the timberline would be covered by forests (Ellenberg, 1996). Accordingly, the zonal vegetation of the submontane belt (between ca. 400 and 700 m) of the Grazer Bergland is dominated by beech forests (Maurer, 1981). However, on steep and rocky slopes facing to the south or southeast, especially on limestone and dolomite, a community complex has developed that may be considered an extrazonal forest-steppe (Paschinger, 1974; Zimmermann, 1976; Niklfeld, 1979; Maurer, 1981; Wendelberger, 1989). These habitats expanded as a consequence of century-long grazing, but similar mosaics of forest and steppe patches certainly did exist prior to human influence, although in a much smaller area (Homann, 1992; Ellenberg, 1996). Given the eastern and southern climatic and vegetation influences, plus the edaphic parameters, these forest-grassland mosaic ecosystems are somewhat similar to the Pannonian forest-steppes.

In the forest-steppes of the Grazer Bergland, single trees or groups of trees (mainly *Pinus sylvestris*, but also *Fagus sylvatica*, *Sorbus aria*, etc.) are scattered in a grassland matrix dominated by *Sesleria caerulea* and *Carex humilis*. The pattern is very similar to the fine-scale mosaics situated on south-facing mountain slopes in the Pannonian region. However, the different dominant tree species (*P. sylvestris* in the eastern Alps and *Quercus pubescens* in the Pannonian region) suggest that substantial differences may also exist between them.

Heterogeneous forest-grassland mosaics have received increased scientific attention recently (e.g. House et al., 2003; Breshears, 2006; Ratnam et al., 2011; Erdős et al., 2014; Hauck et al., 2014). The proportion of wooded versus non-wooded patches is changing due to global, regional and local drivers worldwide (Eldridge et al., 2011). As millennia-long grazing (Maurer, 1981) has been declining in Styria since the 19th century, forests may gradually reconquer some of the grassy habitats. The process is well known in the Pannonian biogeographical region, and it may have serious

consequences on biodiversity (e.g. Centeri et al., 2009; Sărățeanu, Moisuc, 2011). Grazing has presumably played an important role in the past and present state of forest-steppe communities dominated by *Pinus sylvestris* in Austria (Mucina et al., 1993; Kelly, Connolly, 2000). Thus it is increasingly important to gain a better knowledge on the contribution of the forested and non-forested components to the overall diversity of the mosaic landscape. Also, a better understanding of how species composition and diversity are affected by the different proportions of the forested vs. non-forested components seems necessary.

In this study, we wanted to gather information on the spatial organization of the forest-steppes in the Grazer Bergland. Our aim was to characterize the species composition and species richness of forest-grassland mosaic patches with different canopy covers. Our specific objective was to find out whether and how different canopy cover values may affect the herb layer, and to study how herb layer patterns are related to the canopy layer.

MATERIAL AND METHODS

Study area

Our study was carried out in the Grazer Bergland, situated in the eastern part of the Alps, north of the city of Graz (Fig. 1a). We chose three study areas: Zigöllerkogel (N 47°4'17", E 15°4'31"), Pfaffenkogel (N 47°10'0", E 15°18'56") and Gamskogel (N 47°10'33", E 15°17'57") (Fig. 1b). On all three mountains, south facing steep slopes were selected for the field works. Bedrock is limestone (Zigöllerkogel) or dolomite (Pfaffenkogel and Gamskogel), soil is shallow rendzina (Paschinger, 1974; GIS Steiermark, 2016). The mean annual temperature is 9.4 °C (Pilger et al., 2010). The mean annual precipitation is 876 mm (Bärnbach, in the proximity of Zigöllerkogel) and 797 mm (Frohnleiten, in the proximity of Pfaffenkogel and Gamskogel) (Pilger et al., 2010). Traditional land-use of the mountain slopes in the region was grazing, but grazing activity steadily declined during the last 150 years, resulting in forest encroachment (Homann, 1992).

Although zonal vegetation in the submontane zone (ca. 400–700 m) is beech forest, the relatively warm and dry conditions on the south-facing, rocky slopes enable the existence of a mosaic vegetation, which can be identified as the association *Erico-Pinetum sylvestris*, with patches of the associations *Seselietum austriaci* and *Moehringietum bavaricae*.

The grassland component is dominated by *Sesleria caerulea* and *Carex humilis*, other frequent species include *Buphtalmum salicifolium*, *Euphorbia cyparissias*, *Polygala chamaebuxus*, *Teucrium chamaedrys* and *Vincetoxicum hirundinaria*. Cover values often vary between 30 and 70%, except for the most rocky places, where cover is less than 30%.

The forested component is formed by *Pinus sylvestris*, to a lesser degree *Fagus sylvatica* and *Sorbus aria*, scattered individually or in small groves in the grassland matrix. The shrub layer is characterized by *Amelancier ovalis*, *Corylus avellana*, and the young individuals of the trees. The herb layer consists mainly of *Sesleria caerulea* and *Carex humilis*, but *Cyclamen purpurascens*, *Hedera helix* and *Salvia glutinosa* are also typical. Under the dense canopy of *Fagus sylvatica*, the herb layer is usually sparse or almost lacking, elsewhere it has cover values similar to that of the grassland component. Detailed description of the plant associations can be found in Niklfeld (1979) and Eichberger et al. (2007).

Field works

In all study sites (Zigöllerkogel, Pfaffenkogel, Gamskogel), three 25 m × 25 m plots were selected (“large plots”) with different canopy cover values. In each case, the large plots were very close to one another, with the same exposition and similar slope inclination values. Every effort was made to select plots with a more or less even spatial distribution of trees. The following canopy cover grades were available (with a roughly even tree distribution): Zigöllerkogel: 20%, 50%, 75%, Pfaffenkogel: 5%, 20%, 50%, Gamskogel: 5%, 20%, 40%. Every plot was situated within the elevation range 450-650 m.

Within each large plot, twenty 2 m × 2 m plots were established (“small plots”) in a regular arrangement. Coenological relevés were prepared in May and June 2015, by

visually estimating the percentage cover of all vascular plant species of the herb layer. A total of 180 plots was used in this analysis (3 study sites \times 3 canopy cover grades \times 20 relevés).

Plant species names follow Fischer et al. (2008).

Data analyses

Detrended Correspondence Analysis (DCA) (Hill, Gauch, 1980) was carried out to examine the similarity of the relevés. DCA is able to eliminate the arch-effect which would be expected otherwise, given the gradient-like character of our data, extending from relatively open to more closed sites. The ordination was based on presence-absence data, using the software Canoco 5.0 (ter Braak, Šmilauer, 2012; Šmilauer, Lepš, 2014).

To gain information on how distinct or overlapping the species pools of the large plots are, we prepared area-proportional Venn-diagrams, using BioVenn, an on-line Venn-diagram generator (<http://www.cmbi.ru.nl/cdd/biovenn/>).

Diagnostic species preferring different canopy cover values were identified within each study site for the large plots. For this purpose, we calculated the phi coefficient, as one of the most appropriate measures of fidelity (Tichý, Chytrý, 2006). Analyses were carried out with JUICE 7.0 (Tichý, 2002). We excluded nonsignificant diagnostic species with Fisher's exact test.

Species richness was calculated for each small plot. We tested the data for normality with the Shapiro-Wilk test. Per plot species richness was compared between the different canopy covers of the large plots, using the Kruskal-Wallis test. Statistical analyses were done with the program package SPSS 22.0 (SPSS Inc).

RESULTS

In the 180 plots, a total of 121 species was recorded in the herb layer. The DCA-ordination revealed that the vegetation gradient was rather short (gradient length along the first axis: 2.72, along the second axis: 2.62), suggesting that species turnover is not complete among the habitats (Fig. 2). The three study sites were separated along the first DCA axis: The relevés from Zigöllerkogel formed a distinct group. The relevés

from Pfaffenkogel and Gamskogel were less clearly separated from one another. The separation according to the canopy cover values was less obvious, although relevés from the large plots with low canopy covers tend to occur towards the bottom of the scattergram, while relevés from the large plots with higher canopy covers can be found mainly towards the opposite end of the ordination space.

The Venn-diagrams showed that there was relatively small variation according to the canopy cover values (Fig. 3): most species occurred in all canopy cover grades. In the case of Zigöllerkogel (Fig. 3a) and Paffenkogel (Fig. 3b), the diagrams were almost completely symmetrical, but this was not the case for Gamskogel (Fig. 3c). This latter means that the species composition of the large plots with the lowest and highest canopy covers were a bit more distinct on Gamskogel than in the two other sites.

The number of significant ($p < 0.01$) diagnostic species was rather low for most canopy cover values in all study sites (Table 1). Moreover, most of the species that were found diagnostic in one study site did not prove diagnostic in the other cases, even though the majority of the species was present in all three sites. This suggests that, at least in some cases, diagnostic value was due to chance only, rather than reflecting a true association of a given species to a given canopy cover.

Species richness of the small plots did not differ significantly among the different canopy covers (Fig. 4) (Zigöllerkogel: $H=1.814$, $p=0.3999$; Paffenkogel: $H=3.41$, $p=0.1767$; Gamskogel: $H=1.762$, $p=0.4078$). It is worth mentioning that Zigöllerkogel proved to have considerably higher per plot species richness than the other two sites.

DISCUSSION

Forest-grassland ecosystems have been in the focus of research interest recently (e.g. Breshears, 2006; Kirby, 2015). In particular, the coexistence of the woody and herbaceous species raises important questions concerning spatial heterogeneity and temporal dynamics (House et al., 2003). In this paper we investigated forest-steppe like habitats in the eastern Alps of Austria. Our purpose was to scrutinize how the herb layer is affected by different canopy cover values.

In several forest-grassland ecosystems, differences between canopy and intercanopy patches are usually great regarding both abiotic and biotic characteristics (Breshears 2006). However, in this study on eastern Austrian forest-steppe like habitats, we found that the effects of canopy layer on the herb layer are limited. Species composition (Figs. 2 and 3) and species richness (Fig. 4) differed only moderately among the large plots with different canopy covers. To put it another way, the spatial heterogeneity of the canopy and the herb layers did not prove to be closely related. This is in line with the observations of Niklfeld (1979), who stated that a number of plants with high light and low water demands are able to survive under the *Pinus* canopies. It seems probable that factors other than the canopy (e.g. rocky surfaces) have a larger influence on the herb layer. One possible reason for this lies in the characteristics and branching pattern of *Pinus sylvestris*, the main tree species of the mosaic. Despite the unfavorable site conditions, *P. sylvestris* is able to develop a tall and straight trunk. It usually loses its lower branches with age, and its higher branches cover a small area. Therefore, it enables the herb layer to receive a high amount of solar radiation even directly under the trees.

Our analyses have shown that the forest-steppes of the Grazer Bergland, especially those of Pfaffenkogel and Gamskogel are quite species-poor (Fig. 4). In plots of similar sizes, Pannonian forest-steppes proved to be more species rich (Erdős et al. 2011, 2014). One reason for this might be the fact that pre-human grasslands must have existed in the Grazer Bergland only in the form of small islands within a forest matrix, which certainly limited the number of grassland-related species. In contrast, it is presumed that the Pannonian region had much larger areas of primary grasslands, enabling a higher species richness. In addition, it has to be emphasized that the Grazer Bergland has considerably lower mean annual temperature and higher mean annual rainfall than most of the Pannonian biogeographical region. Thus, whereas Pannonian forest-steppes are determined by climate to a considerable extent, Styrian forest-steppes depend much more on rocky soil conditions. As the humid and cool climate of the Styrian mountains does not favor steppe species, this may contribute to the low species richness values. Nevertheless, the studied vegetation mosaic is extremely important from a conservation

point of view, as it serves as a habitat for some species that cannot tolerate the conditions within the closed beech forests. In addition, forest-steppe habitats enhance habitat diversity and are important components of landscapes.

According to Niklfeld (1979), the naturally treeless patches within the community *Erico-Pinion sylvestris* are less diverse than similar habitats under an anthropogenic influence and/or of secondary origin. Thus it is possible that the site of Zigöllerkogel has a larger human influence (e.g. a more recent history of grazing) than the other two sites. An alternative explanation of the considerably higher species-richness may be the higher amount of rocky surfaces, which creates micro-habitats for some species that cannot compete with dominant grasses. Of course, the two forces may operate simultaneously, maybe with additional factors, such as the effects of bedrock.

Not only did the relevés from Zigöllerkogel have a higher species richness, but also their composition was quite distinct, forming a well-defined group in the DCA ordination scattergram (Fig. 2.). Here, the factors mentioned above (human influence, rocky surfaces) may contribute to this difference. In addition, the role of the different bedrocks should be emphasized, as it may result in different species composition (Gams, 1930).

Our results suggest that, if forest cover is increasing due to land-use changes in the Grazer Bergland, the process presumably does not have a potential to immediately alter the species composition of the mosaic habitat complex. In the studied ranges, there were no clear differences between the herb layers under different canopy cover values, indicating that most species are able to survive even under the tree canopies or in the remaining small grassland patches. Similarly, in a Pannonian forest-steppe mosaic, forest canopy cover more than doubled within 40 years, being well above 20% in 2005. However, typical species of the grassland patches continue to flourish (Erdős et al., 2013a). Moreover, in another forest-steppe (where grazing ceased considerably earlier), canopy cover increased to ca. 73% (Erdős et al., 2015a), but grassland-related species are obviously able to survive even in the remaining, relatively small grassland patches (Erdős et al. 2013b), and, to a certain degree, even within the forest patches (Erdős et al., 2015b).

Nevertheless, the importance of a heterogeneous forest-steppe cannot be overestimated, thus the vegetation alterations following the land-use changes should be monitored. Every effort should be made to conserve these valuable habitats, and in case of a vigorous forest encroachment, the re-establishment of grazing should be considered a possible management for conservation purposes.

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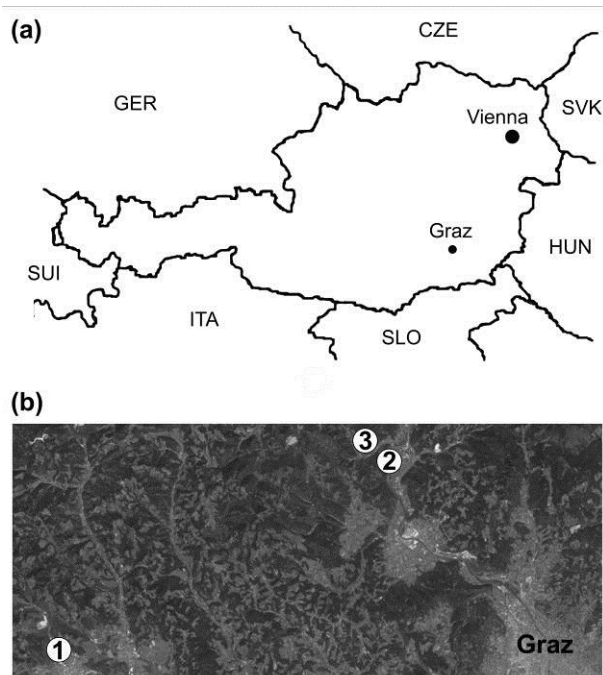


Fig. 1. (a) The location of Graz in Austria. (b) The location of the three study sites in the Grazer Bergland. 1: Zigöllerkogel, 2: Pfaffenkogel, 3: Gamskogel (from Google Earth).

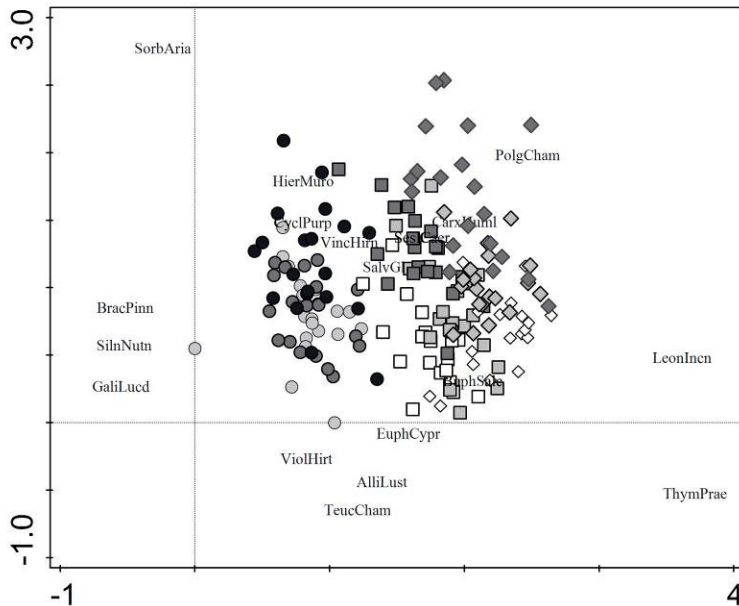


Fig. 2. DCA ordination biplot of the 180 coenological relevés and the most important 18 species. Percentage variances explained by the first and second DCA axes were 10.83 and 6.42%, respectively. Circles: Zigöllerkogel, squares: Pfaffenkogel, diamonds: Gamskogel. Symbol colors vary according to canopy cover values of the large plots; colors darken with increasing cover values. AlliLust: *Allium lusitanicum*, BracPinn:

Brachypodium pinnatum, BuphSalc: *Bupthalmum salicifolium*, CarxHuml: *Carex humilis*, CyclPurp: *Cyclamen purpurascens*, EuphrCypr: *Euphorbia cyparissias*, GaliLucd: *Galium lucidum*, HierMuro: *Hieracium murorum*, LeonIncn: *Leontodon incanus*, PolgCham: *Polygala chamaebuxus*, SalvGlut: *Salvia glutinosa*, SesiCaer: *Sesleria caerulea*, SilnNutn: *Silene nutans*, SorbAria: *Sorbus aria*, TeucCham: *Teucrium chamaedrys*, ThymPrae: *Thymus praecox*, VincHirn: *Vincetoxicum hirundinaria*, ViolHirt: *Viola hirta*.

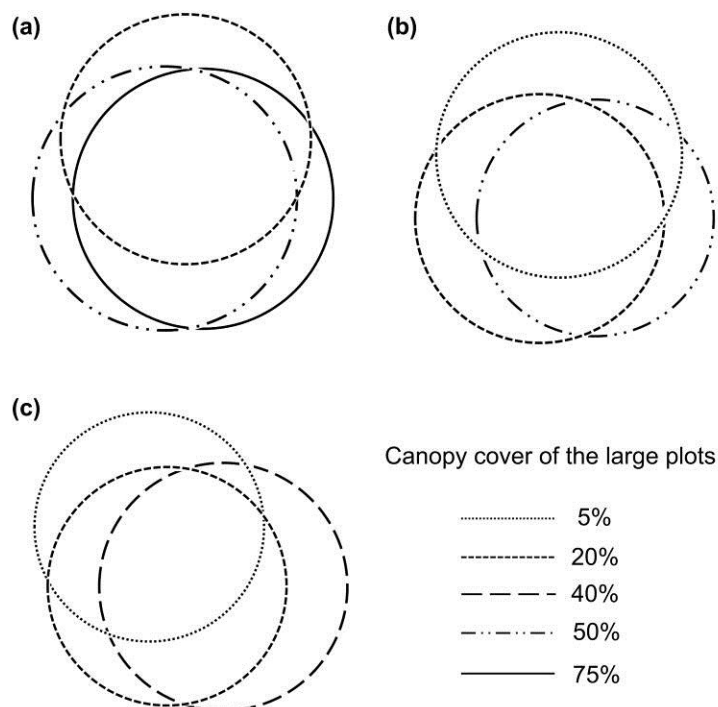


Fig. 3. Area-proportional Venn-diagrams of the species pool of the large plots with different canopy covers. (a) Zigöllerkogel, (b) Pfaffenkogel, (c) Gamskogel. Note that diagrams are proportional within, but not among the panels.

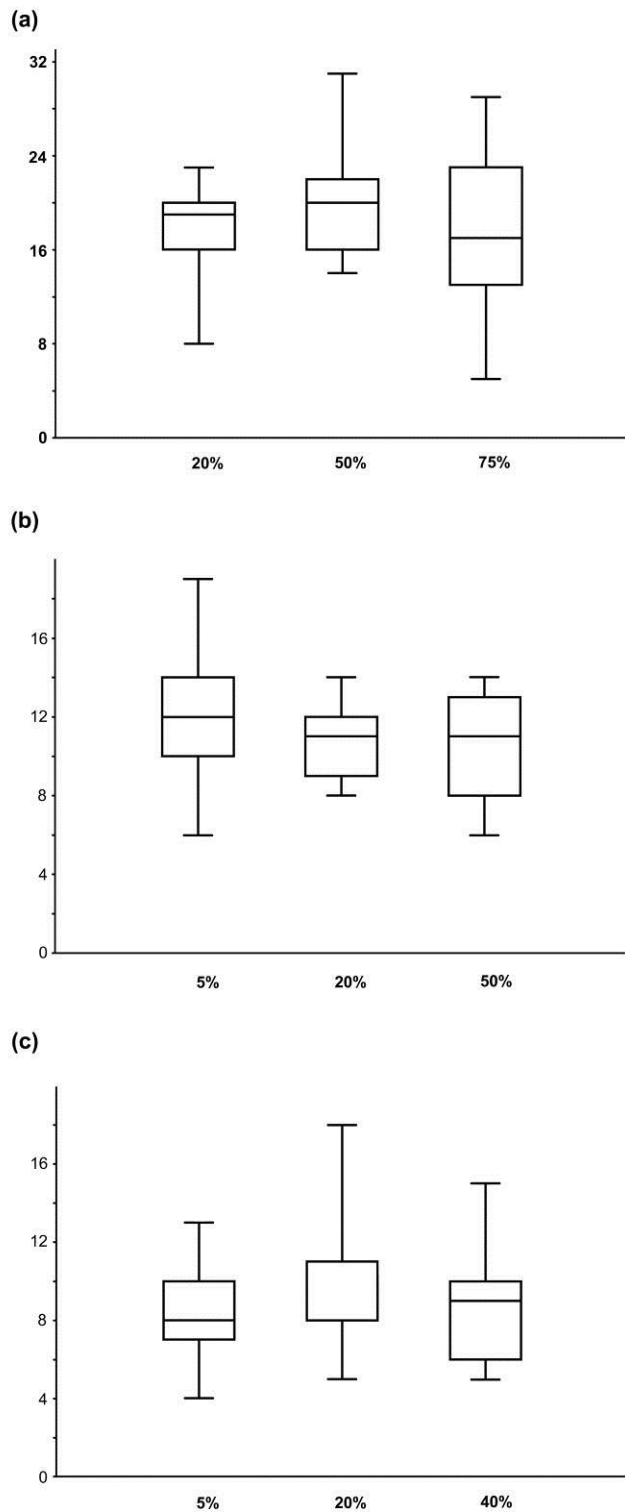


Fig. 4. Species richness per small plots under different canopy covers. (a) Zigöllerkogel, (b) Pfaffenkogel, (c) Gamskogel.

Table 1. Phi coefficients of the significant ($p < 0.01$) diagnostic species of the large plots with different canopy covers.

	Canopy cover		
Zigöllerkogel	20%	50%	75%
<i>Hieracium pilosella</i> agg.	0.640		
<i>Carex digitata</i>	0.478		
<i>Polygala chamaebuxus</i>	0.414		
<i>Cephalantera damasonium</i>	0.397		
<i>Cirsium arvense</i>	0.397		
<i>Leontodon incanus</i>	0.388		
<i>Hieracium bauhini</i>		0.562	
<i>Asplenium ruta-muraria</i>		0.409	
<i>Taraxacum</i> sect. <i>Ruderalia</i>		0.400	
<i>Cyclamen purpurascens</i>		0.354	
<i>Asplenium trichomanes</i>			0.433
Pfaffenkogel	5%	20%	50%
<i>Allium lusitanicum</i>	0.476		
<i>Euphorbia cyparissias</i>	0.315		
<i>Salvia glutinosa</i>	0.304		
<i>Thymus praecox</i>	0.304		
<i>Silene nutans</i>		0.397	
<i>Picea abies</i>			0.493
<i>Hedera helix</i>			0.443
<i>Epipactis atrorubens</i>			0.397
<i>Juglans regia</i>			0.397
<i>Hieracium murorum</i>			0.346
Gamskogel	5%	20%	40%
<i>Hieracium lachenalii</i>	0.447		
<i>Asplenium ruta-muraria</i>	0.397		
<i>Festuca heterophylla</i>	0.397		
<i>Thymus praecox</i>	0.354		
<i>Salvia glutinosa</i>		0.528	
<i>Hieracium bifidum</i>		0.434	
<i>Viburnum lantana</i>			0.602
<i>Amelanchier ovalis</i>			0.528
<i>Bromus erectus + pannonicus</i>			0.397