

Grazing promotes bryophyte species richness in semi-natural grasslands

Tuomo Takala^{1,*}, Teemu Tahvanainen¹ & Jari Kouki²

¹ Department of Biology, University of Eastern Finland, Joensuu Campus, Yliopistokatu 7, P.O. Box 111, FI-80101, Joensuu, Finland (*corresponding author's e-mail: tuomot@student.uef.fi)

² School of Forest Sciences, University of Eastern Finland, Joensuu Campus, Yliopistokatu 7, P.O. Box 111, FI-80101, Joensuu, Finland

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We studied the effects of cattle grazing on bryophyte species richness in Finnish semi-natural grasslands and examined if there are differences among bryophyte life-strategies in relation to grazing pressure. We recorded species richness and cover of bryophytes in 420 sample plots located in 21 grasslands. Percentage of bare ground, height of vascular plant vegetation and cover of vascular plant litter were used as proxies for grazing intensity. We also explored the microhabitat preferences of individual species. Species richness of all bryophytes, perennial residents and colonists increased with grazing pressure. As compared with perennials, many species among the colonists had strong affinity to sites with high proportion of bare ground. We conclude that both perennial and colonist bryophytes benefit from grazing in semi-natural grasslands, although the effects of grazing are differently realized in the different bryophyte groups.

Introduction

Effects of grazing on vascular plant diversity are usually positive in productive environments like mesic grasslands (Proulx & Mazumder 1998), although negative effects of severe overgrazing are also evident (Jantunen *et al.* 2003). The positive effects of grazing are potentially attributable to the survival of many subordinate life-forms that are absent or scarce in overgrown vegetation (Pykälä 2004, Johansson *et al.* 2010). Much less is known about the effects of grazing on co-occurring species groups that are not eaten by grazers although these can form a substantial part of the biodiversity in grazed ecosystems.

Bryophytes are foraged by few animals (Prins 1981), nevertheless they can be indirectly affected by grazing. Indeed, bryophyte diversity is low in abandoned grasslands and re-establishment of grazing can help to restore the community structure and diversity (Takala *et al.* 2012). In addition, processes associated with grazing (e.g., trampling, urinating and defecating) can all affect vegetation directly or indirectly (Kohler *et al.* 2006). In this study, we concentrate on the effects related to the changes in vascular plant biomass and ground disturbances and how they affect bryophyte species richness and cover. The suppression of competition by removal of plant biomass and by increase of ground disturbance is hypothesized to increase

vascular plant diversity (Grime 1977, Huston 1979, During & Willems 1984). The same two mechanisms are suggested to affect bryophyte diversity in productive environments (van Tooren *et al.* 1990). Indeed, vascular plants play a significant role in determining the growth conditions for bryophytes by strong competition for space (Virtanen *et al.* 2000, Bergamini *et al.* 2001, Aude & Ejrnaes 2005). Mowing experiments revealed that exposure of mineral ground is especially important to bryophyte richness (van Tooren *et al.* 1990, Vanderpoorten *et al.* 2004).

Many recent studies on the effects of grazing on plant communities have focused on the scale dependence of diversity patterns (e.g. Bello *et al.* 2007) and it has been pointed out that studies concentrating only on one spatial scale of species richness or diversity can produce misleading results (Giladi *et al.* 2011). We take this into account by studying the effects of grazing on bryophyte species richness at both plot and grassland scales.

Bryophytes differ from vascular plants in many morphological, physiological and life-cycle characteristics (During 1979, 1992, Proctor 2008, Rydin 2008). There are, however, remarkable ecological differences also among bryophytes and species with different life-history characteristics may show different responses to grazing. However, the exact mechanisms of grazing effects and group-specific responses are not understood among the grassland bryophytes. In this study, we apply a life strategy classification of bryophytes (During 1979, 1992) that is based on species adaptations to (1) substrate properties in terms of longevity and predictability, (2) the frequency of favorable periods and (3) the distances between available substrate patches. Obviously, there are inherent connections to ground disturbances and vascular plant competition, in addition to the dispersal capability of species.

We concentrate on two questions: (1) How does cattle grazing affect bryophyte species richness in Finnish semi-natural grasslands at different scales? (2) Do bryophyte species with differing life-history strategies respond differently to grazing? In this study, species richness is taken as a measure of biodiversity.

The bryophyte nomenclature follows Ulvinen *et al.* (2013).

Material and methods

Study site and experimental design

The mesic, semi-natural grasslands of the study are located on the steep (15°–25°) river valley slopes of the Rekijoki and its side brooks in southwestern Finland (60°30'N, 23°25'E). The area is situated in the southernmost fringe of the south-boreal vegetation zone (Kalliola 1973). The area belongs to the ancient seabed of various Baltic Sea stages and is characterized by the thick and homogenous layers of deposited clay (Aartolahti 1975).

For the study, we selected 21 unfertilized grasslands. All of them were effectively without stones and boulders, and open or with only scattered shrubs or trees (mainly *Juniperus communis*). The grasslands included sites where grazing had continued uninterrupted for at least 50 years ($n = 7$), previously abandoned grasslands where grazing had been re-established 15–25 years before the sampling ($n = 7$), and grasslands that had been abandoned 25–45 years ago ($n = 7$). With varying grazing histories, these 21 grasslands represent a wide gradient from formerly-grazed to still intensively-grazed pastures (*see* Takala *et al.* 2012). The continuously grazed and re-established grasslands were seasonally (in the summer) grazed by cattle. With this set of different grasslands we could estimate the effects of grazing at the time scale of decades. Unfortunately, we could not document the actual grazing pressure which, in fact, is changing from year to year. Consequently, our study focuses on long-term grazing pressures and land-uses rather than on short annual changes in local grazing patterns.

We randomized 20 plots (60 × 60 cm) in each of 21 grasslands and estimated visually the covers of bryophyte species in each plot. Bryophytes were identified to the species level excluding *Dicranella* and/or *Trichodon* species, which were treated as one taxon. From here on all the taxa are called species. In each plot, we also measured the height of vegetation (cm), cover of vascular plant litter (%), cover of graminoid species (%), cover of herbaceous species (%) and the percentage of bare ground. Height of vegetation was calculated as a mean of five

measurements (accuracy of ± 5 cm in each plot). These five variables were selected to represent the effects of grazing in the grasslands and used to explain the perceived bryophyte richness. We carried out the measurements in July 2009.

The effect of grazing, as a latent variable, cannot be measured directly. We used height of vegetation and cover of litter as surrogate measures of reduction in vascular plant biomass. Height of vegetation was a measure of the prevailing grazing pressure, however it was apparently also affected by grazing in previous years through the changes in growth forms and species compositions resulting from grazing (Pykälä 2004). The cover of litter reflects, in particular, the grazing pressure of previous years. We included the covers of herbaceous and graminoid species in the study because continuous grazing can change the vascular plant composition. In the study region, abandonment of grasslands generally leads to an increasing dominance of graminoids, and continuous grazing to an increasing cover of small herbaceous plants (Pykälä 2004). Grazing can also increase percentage of bare ground, especially in arid environments (Bello *et al.* 2007). Our study region is humid but there were still numerous patches of bare ground. Occasional anthill sides were the only other source of bare ground in the grasslands as there were no marks of recent landslides or remarkable erosion in the study plots.

Analyses

We grouped the bryophyte species into the life-strategy groups of During (1979, 1992) using the species classification of Dierssen (2001) (Table 1). Among the life-strategy groups, perennials and colonists were sufficiently species-rich to be included in statistical analyses.

We calculated the species richness and cover for all bryophytes and for the life-strategy groups separately and partitioned the species richness into gamma (S_γ), beta (S_β) and alpha (S_α) components. S_γ was the total species richness of the 20 sample plots in each of the 21 grasslands, while S_α represents the average species richness of plots in each grassland (species density). S_β is defined as S_γ/S_α (Tuomisto 2010) and we used it

as an inverse measure of turnover between the plots. Small S_β values mean a great disparity between S_γ and S_α and presumably a greater species turnover among the plots.

All five independent variables had to be transformed to meet the assumptions of parametric testing. The litter, graminoids and herbaceous-species cover values were log-transformed, height of vegetation and percentage of bare ground were square-root-transformed. Based on strong correlations (> 0.80) between the independent variables (Table 2) and because some of the variables were mutually exclusive (percentage of bare ground, cover of litter), we decided to use principal component analysis (PCA) in order to convert the variables into a smaller set of orthogonal principal components. This was also ecologically rational, as we were studying the effects of grazing as a complex gradient. We used correlation matrix as a cross-products matrix and applied varimax rotation in PCA. Extracted components were then used as independent variables in linear regression analyses of the effects of grazing on the bryophyte species richness (S_γ , S_β , S_α) and average cover in the grasslands ($n = 21$). PCA was performed using SPSS 17.0 (ver. 17.0., SPSS Inc., Chicago).

Finally, we compared the life-strategy groups by exploring the distribution patterns of individual species along the gradients of exposure of bare ground, height of vascular vegetation and cover of litter (Fig. 1). We calculated abundance-weighted arithmetic averages of each of these three microhabitat variables for each species using species abundances as weights, hence the resulting values depict the centroids of species distribution along the gradients of each microhabitat variable. Species occurring in fewer than three plots were rejected from the analysis. Differences in the abundance-weighted averages between perennials and colonists were tested with a *t*-test.

Results

We found 42 moss species in the studied grasslands (Table 1). Most species were classified as perennials (20) or colonists (17) but in addition five shuttle species were recognized. All the

shuttle species and 15 of the 17 colonists were acrocarpous (i.e. having the archegonia at the top of the stem) while 16 of the 20 perennials were pleurocarpous (i.e. having the archegonia on short lateral branches). In the data, 85% of the total bryophyte cover and 48% of the total number of species were perennials. Respective values for colonists were 14% of the total bryophyte cover and 40% of the total species number. Species richness of perennials (S_γ , S_β , S_α) and cover of perennials correlated with species richness of colonists (S_γ , S_β , S_α) and cover of colonists, respectively (Table 2). The species

richness (S_γ , S_β , S_α) and cover of all bryophytes and of bryophyte groups also correlated strongly with the cover of bare ground, the vegetation height and the cover of litter. Liverworts or hornworts were not found in the study plots.

PCA resulted in significant compression of information from the original data (Bartlett $\chi^2 = 76.06$, $p < 0.001$; KMO = 0.66). In the analysis, all communalities were over 0.85, i.e. the variances of the independent variables were accurately represented with the extracted principal components. Two-component rotated solution was selected for the analysis, the first component

Table 1. Classification of the found bryophyte species into the life-strategy groups (During 1992) according to Dierssen (2001). Species occurrences in the grasslands and in the study plots are given after each species name (occurrences in the grasslands/plots). There were 21 grasslands and 420 plots in the study.

Spores	Potential life span (yr)/Reproductive effort		
	Many/Low	Few/Medium	< 1/High
Numerous, very light (< 20 μm)	Perennial residents	Colonists	Fugitives
	Perennials	Ephemeral colonists	
	<i>Abietinella abietina</i> 7/21	<i>Bryum rubens</i> 9/30	
	<i>Amblystegium serpens</i> 12/121	<i>Bryum violaceum</i> 6/8	
	<i>Brachytheciastrum velutinum</i> 1/1	<i>Fissidens viridulus</i> 7/13	
	<i>Brachythecium albicans</i> 19/179		
	<i>Brachythecium campestre</i> 6/7	Colonists S.S.	
	<i>Brachythecium erythrorrhizon</i> 3/3	<i>Barbula unguiculata</i> 12/30	
	<i>Brachythecium mildeanum</i> 12/52	<i>Bryum argenteum</i> 3/4	
	<i>Thuidium assimile</i> 14/36	<i>Bryum caespiticium</i> 7/17	
	<i>Bryum moravicum</i> 3/8		
	<i>Ceratodon purpureus</i> 12/38		
	<i>Dicranella/Trichodon</i> sp. 10/13		
	<i>Fissidens bryoides</i> 1/1		
	<i>Rhodobryum roseum</i> 3/3		
	<i>Syntrichia ruralis</i> 12/66		
	<i>Weissia controversa</i> 6/9		
	Pioneers		
	<i>Bryum elegans</i> 1/4		
	<i>Pohlia nutans</i> 1/1		
	<i>Brachythecium salebrosum</i> 20/63		
	<i>Oxyrrhynchium hians</i> 2/2		
	Stress-tolerant perennials		
	<i>Hypnum cupressiforme</i> 2/2		
	<i>Sciuro-hypnum starkei</i> 1/1		
	<i>Thuidium recognitum</i> 1/1		
Few, large (> 20 μm)	Dominant	Short-lived shuttle	Annual shuttle
	–	<i>Atrichum undulatum</i> 1/1	<i>Phascum cuspidatum</i> 2/5
		<i>Bryum pallens</i> 2/2	<i>Tortula truncata</i> 16/36
	Long-lived shuttle		
	<i>Rhizomnium punctatum</i> 15/58		

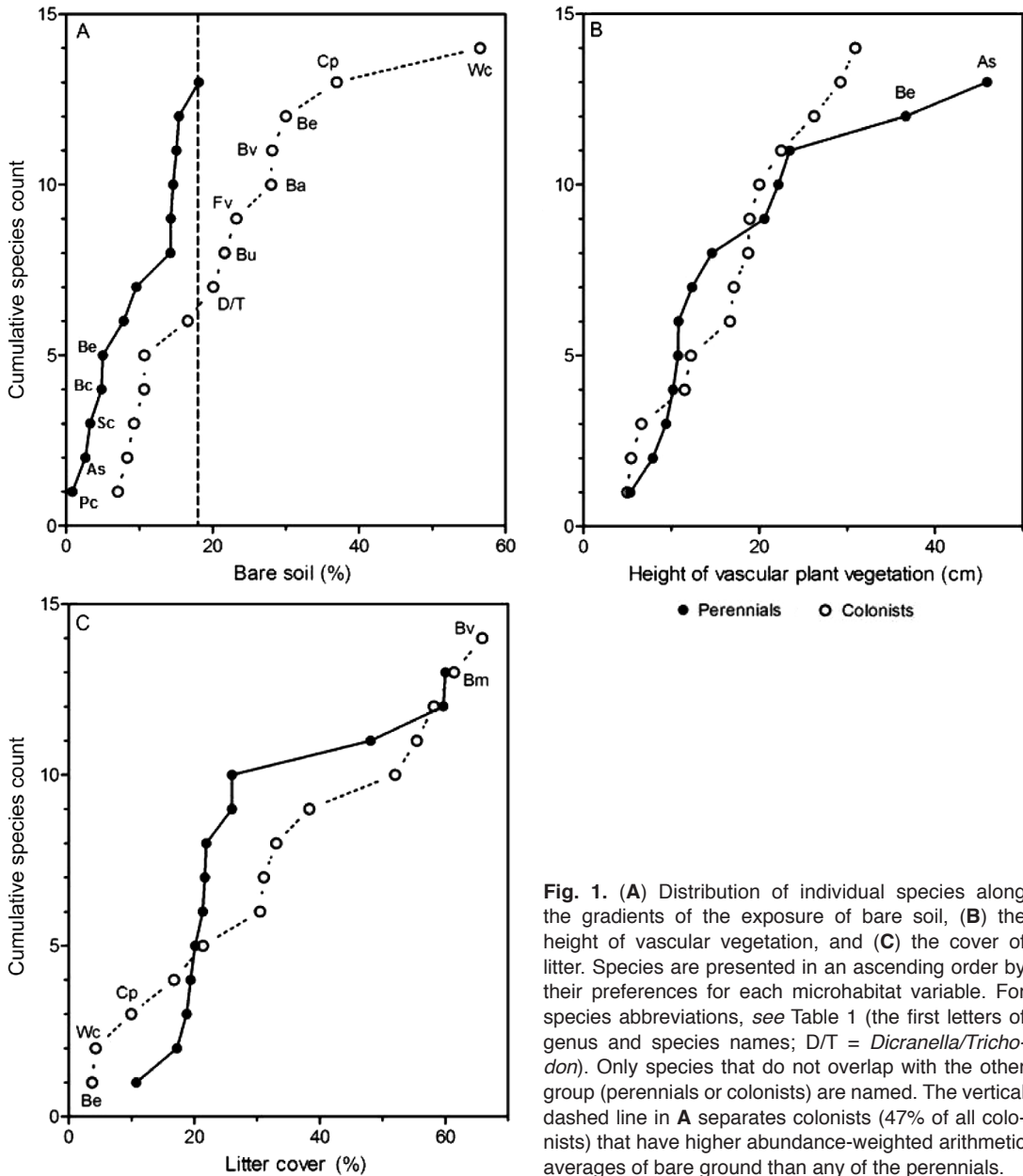


Fig. 1. (A) Distribution of individual species along the gradients of the exposure of bare soil, (B) the height of vascular vegetation, and (C) the cover of litter. Species are presented in an ascending order by their preferences for each microhabitat variable. For species abbreviations, see Table 1 (the first letters of genus and species names; D/T = *Dicranella/Trichodon*). Only species that do not overlap with the other group (perennials or colonists) are named. The vertical dashed line in **A** separates colonists (47% of all colonists) that have higher abundance-weighted arithmetic averages of bare ground than any of the perennials.

(PC1) representing 58.3% and the second (PC2) 31.9% of the total variance (together 90.2%). PC1 comprised percentage of bare ground (factor load -0.93), cover of litter (0.93) and vegetation height (0.87); PC2 cover of herbaceous species (0.93) and cover of graminoids (-0.78).

In the linear regression analyses, all bryophytes, perennials and colonists gave very similar results. Species richness (S_γ , S_β , S_α) and

average cover of all groups were significantly explained by the linear models with the principal components (PC) as independent variables (Table 3). PC1 had significant effects in all cases, whereas PC2 affected only S_β of the groups and S_α of all bryophytes. As the value of PC1 increased (percentage of bare ground decreased, vegetation height and cover of litter increased), S_γ , S_α and average cover decreased, while S_β

increased (Figs. 2–4). Linear relationships were very clear in all bryophytes and perennials, and somewhat weaker in colonists (Table 3). Interestingly, S_β was always explained also by PC2 (Table 3). As PC2 increased (the cover of graminoids decreased, the cover of herbaceous species increased), S_β decreased as indicated by its consistently negative values (Table 3).

Abundance-weighted averages of the microhabitat variables calculated for each species revealed that as compared with perennials, colonists occupied the plots with higher percentage of bare ground: 47% of the colonist species had higher abundance-weighted average of bare ground than any of the perennials (Fig 1). The difference between the groups was significant (t -test: $t_{25} = 2.99$, $p = 0.006$). We did not find any clear differences between perennials and colonists in the species distributions along the gradients of height of vegetation (t -test: $t_{25} = 0.12$, $p = 0.903$) and cover of litter (t -test: $t_{25} = 0.80$, $p = 0.433$).

Discussion

The effects of grazing on bryophyte richness and cover

Perennial and colonist species represented the

main life-strategy groups in the grasslands of this study. As per the cover of bryophytes, perennials were the dominant group, however colonists were almost as species-rich. The abundance of colonists was clearly higher in this study than that reported by Vanderpoorten *et al.* (2004) for mown grasslands in Belgium. The shuttle-species groups in this study included only few species and only two shuttle species were relatively frequent in the pastures. This may in one part be due to the short life-span of vegetative shoots especially of annual shuttle-species, which makes them difficult to identify in a non-recurrent inventory. Nonetheless, they have been found but in very low numbers in above-ground vegetation of pastures also in other studies (van Tooren *et al.* 1990). The species richness (S_γ , S_β , S_α) of both colonists and perennials correlated positively with the cover of all bryophytes indicating that the total cover of bryophytes can be used as an estimate of bryophyte diversity in grasslands.

The first principal component (PC1) represents the main grazing intensity gradient. Greater values of PC1 indicate lower effect of grazing, as evidenced by increasing cover of litter, higher vascular-plant vegetation and decreasing percentage of bare ground. The factor loads and communalities showed that these strongly correlated variables had strong effects on the PC1. Also

Table 3. Statistics of the linear regression models with principal components (PC) as independent variables. Component coefficients differing significantly from zero are those whose $p < 0.05$. $n = 21$.

	Adjusted r^2	ANOVA $F_{2,18}$	Coefficients		
			β (Constant)	β_1 (PC1)	β_2 (PC2)
All species					
S_γ	0.57	14.00 ($p < 0.001$)	14.62 ($p < 0.001$)	-4.41 ($p < 0.001$)	0.60 ($p = 0.485$)
S_α	0.87	67.28 ($p < 0.001$)	2.75 ($p < 0.001$)	-1.56 ($p < 0.001$)	0.30 ($p = 0.043$)
S_β	0.73	28.42 ($p < 0.001$)	7.33 ($p < 0.001$)	3.29 ($p < 0.001$)	-2.04 ($p = 0.001$)
Average cover	0.78	35.67 ($p < 0.001$)	0.22 ($p < 0.001$)	-0.18 ($p < 0.001$)	0.01 ($p = 0.623$)
Perennials					
S_γ	0.53	12.41 ($p < 0.001$)	7.52 ($p < 0.001$)	-2.26 ($p < 0.001$)	0.30 ($p = 0.521$)
S_α	0.83	49.97 ($p < 0.001$)	1.76 ($p < 0.001$)	-1.03 ($p < 0.001$)	0.20 ($p = 0.077$)
S_β	0.67	21.67 ($p < 0.001$)	6.28 ($p < 0.001$)	3.26 ($p < 0.001$)	-2.45 ($p = 0.001$)
Average cover	0.71	25.36 ($p < 0.001$)	0.19 ($p < 0.001$)	-0.16 ($p < 0.001$)	0.002 ($p = 0.938$)
Colonists					
S_γ	0.32	5.75 ($p = 0.012$)	5.48 ($p < 0.001$)	-1.74 ($p = 0.003$)	0.08 ($p = 0.878$)
S_α	0.41	8.05 ($p = 0.003$)	0.74 ($p < 0.001$)	-0.40 ($p = 0.001$)	0.04 ($p = 0.681$)
S_β	0.40	7.72 ($p = 0.004$)	9.40 ($p < 0.001$)	2.56 ($p = 0.012$)	-2.52 ($p = 0.013$)
Average cover	0.34	6.25 ($p = 0.009$)	0.03 ($p < 0.001$)	-0.021 ($p = 0.004$)	0.008 ($p = 0.226$)

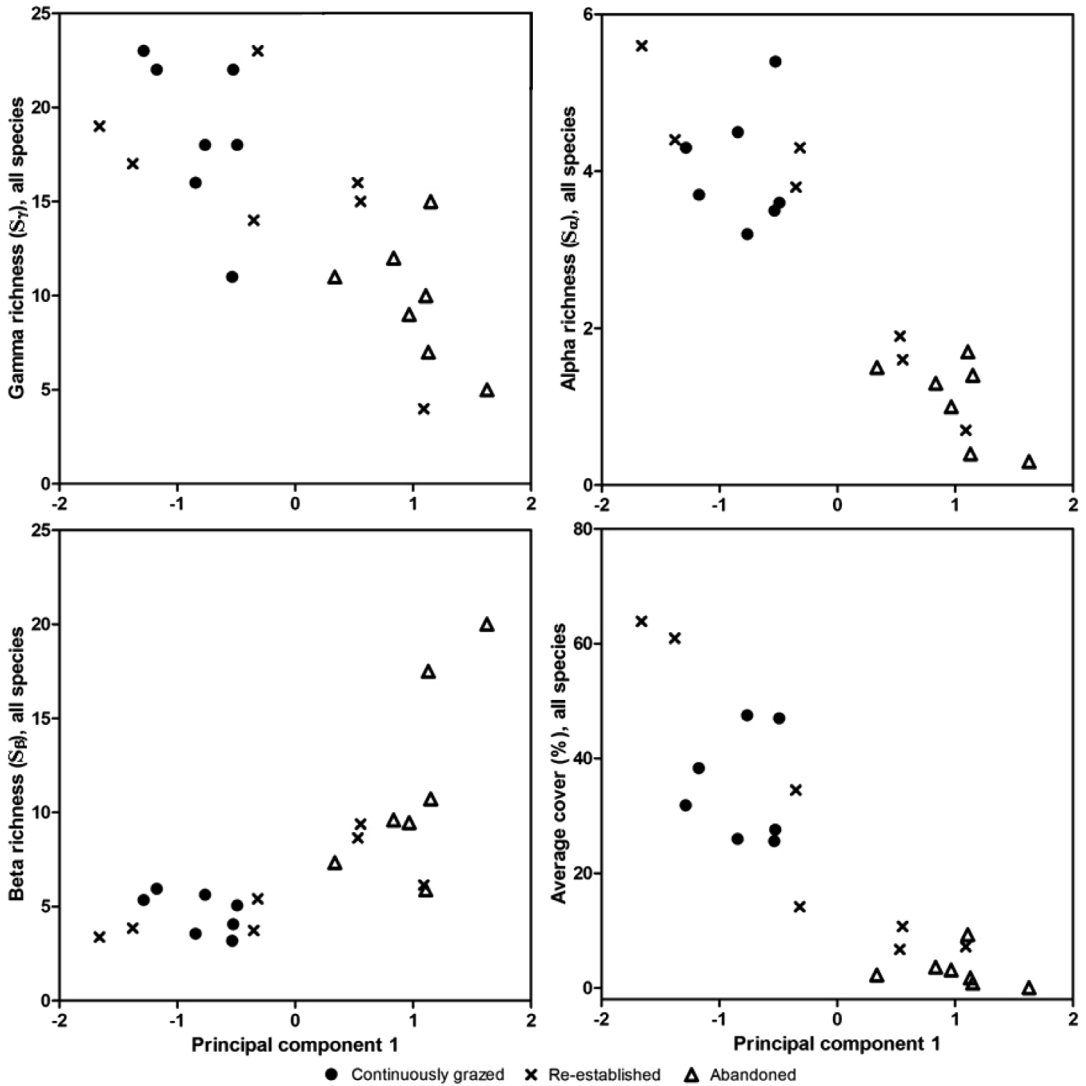


Fig. 2. Relationships between the species richness (S_γ , S_β , S_α) and cover of all bryophytes and PC1. The cover of bare ground has a negative effect while the vegetation height and cover of litter have positive effects on the values of the component.

the second principal component (PC2) was well interpretable as representing a structural gradient of vascular-plant vegetation between herbaceous- and graminoid-plant cover. The PC1 explained to a large extent the variation in species richness and cover of bryophytes in the grasslands, indicating a generally positive effect of grazing. Also the strong correlations between the original independent variables and the species richness and cover of bryophytes were in line with our interpretation of the PC1 pattern (see Table 2).

The positive effect of grazing on species richness of bryophytes was evident at both spatial scales used in this study (S_γ and S_α). S_γ was slightly more affected by PC1 than S_α but their patterns were essentially similar. The relationship between PC1 and S_β was negative, indicating that turnover between the plots was greater in grasslands with greater grazing intensity. This can be a sign of microhabitat heterogeneity. If there is a lot of bare ground, species count per plot can be low even if grazing at a larger scale

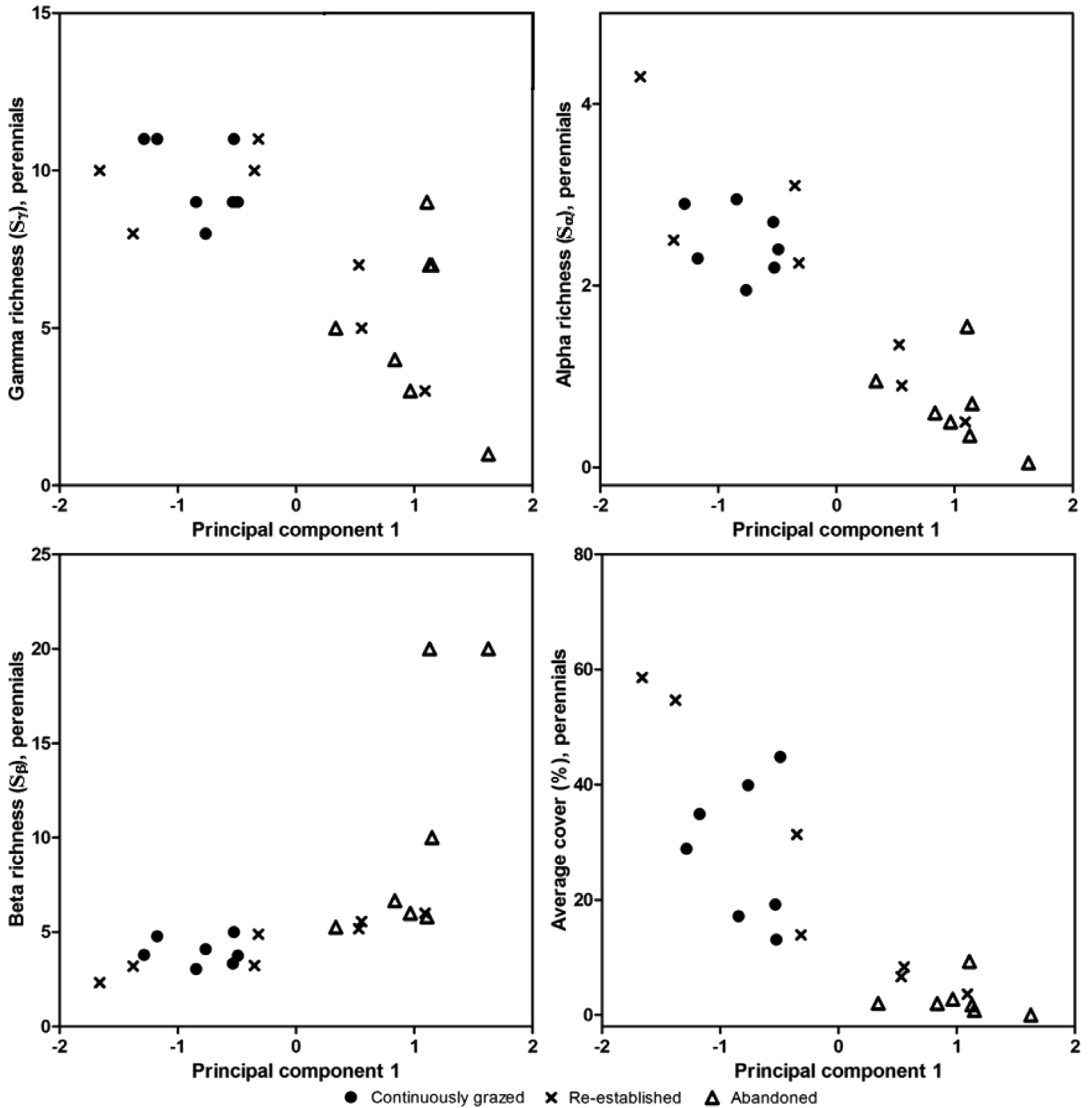


Fig. 3. Relationships between the species richness (S_γ , S_β , S_α) and cover of perennials and PC1. The cover of bare ground has a negative effect while the vegetation height and cover of litter have positive effects on the values of the component.

promotes species richness by increasing micro-habitat heterogeneity (Bello *et al.* 2007).

We interpret the main grazing-related gradient in our data (PC1) as a gradient of inter-specific competition and disturbance. Prevailing competition and disturbances, in addition to environmental stress, are recognized as fundamental forces determining species traits in plant communities (Grime 1977, 2001). According to Huston's (1979, 1994) dynamic equilibrium model, environment disturbances and productiv-

ity determine the level of competition and thus diversity. The height of vegetation and the cover of litter are proxies for vascular plant biomass, and percentage of bare ground is a measure of disturbance. Shading by vascular plants presumably is an important mode of pre-emptive competition acting against bryophytes in grasslands. Indeed, light competition between bryophytes and vascular plants is often very asymmetrical (Chapman & Rose 1991, Mayer *et al.* 2009) and shading by plant litter can also hamper the

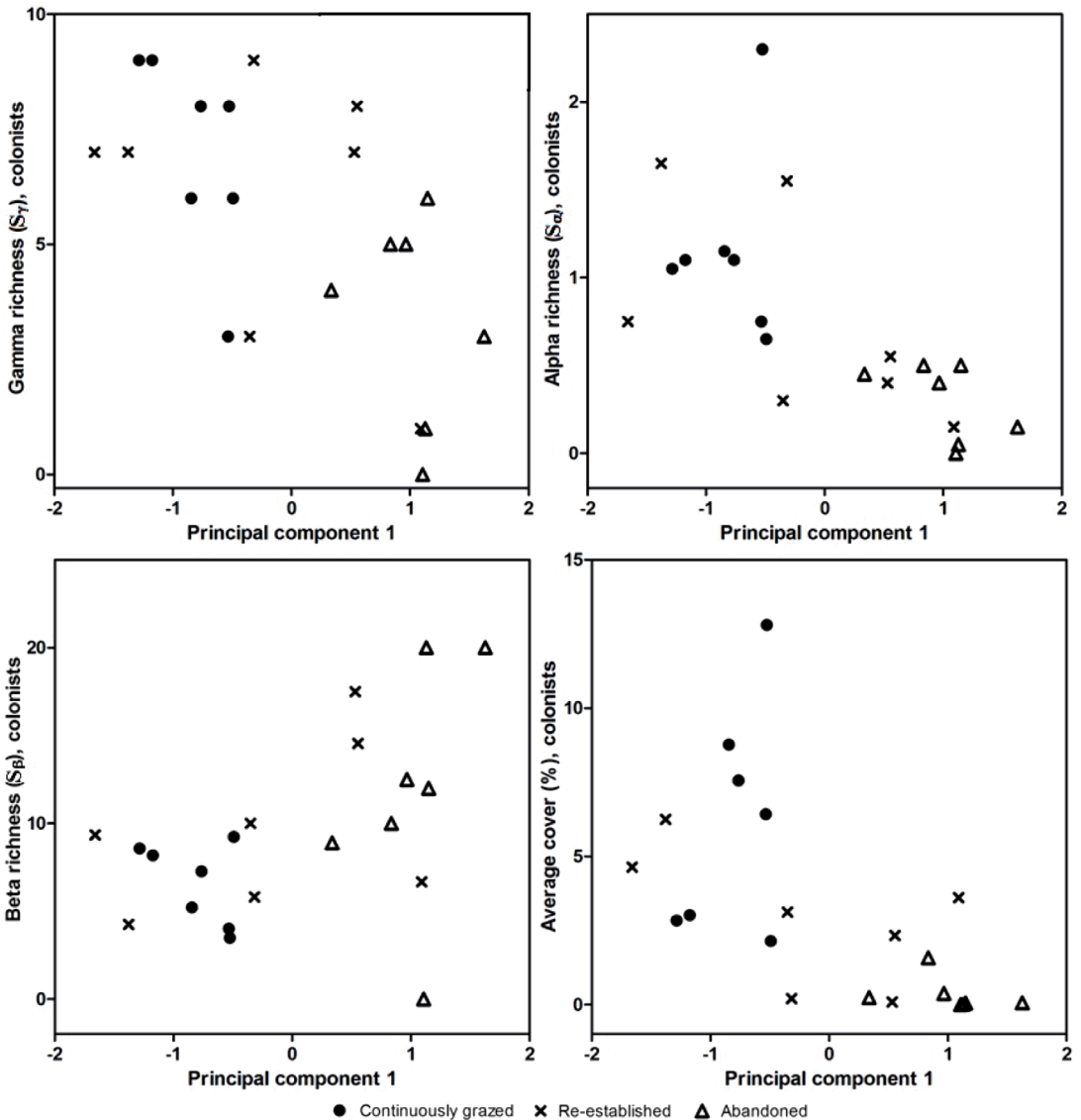


Fig. 4. Relationships between the species richness (S_γ , S_β , S_α) and cover variables of colonists and PC1. The cover of bare ground has a negative effect while the vegetation height and cover of litter have positive effects on the values of the component.

growth of bryophytes (Noy-Meir 1989, Chapman & Rose 1991, Mayer *et al.* 2009). We suggest that grazing increases the species richness of bryophytes, in part, by decreasing competition from vascular plants. Another potential mechanism is positive disturbance by generation of openings in the vascular-plant layer resulting from animal trampling.

Intensively-grazed grasslands with a high bryophyte-species richness and cover had high

percentages of bare ground in our grazing-intensity gradient. Following the hypothesis of intermediate disturbances (Grime 1977, 2001, Connell 1978, Huston 1979), too intensive grazing should lead to a decrease in diversity. However, in this study we did not find any reduction in species richness resulting from high grazing intensities in the semi-natural grasslands. The relationship between the grazing-intensity gradient and species richness at both scales (S_γ and S_α) was

monotonic instead of hump-backed. The species richness of vascular plants exhibited a similar pattern when studied with the same set of grassland categories and in the same area (Pykälä 2005). In fact, the peak in diversity predicted by the intermediate disturbance hypothesis is rarely found in empirical studies, and the relevance of the hypothesis is moot (Fox 2013). However, in this study grazing pressure appeared to be at a sustainable level in the grasslands, as far as the diversity of plant communities is considered.

While most results were explained to a high degree by the PC1 depicting main effect of grazing pressure, PC2 explained S_{β} of bryophyte species almost as well. The relationship was negative, indicating a decrease in S_{β} (increasing turnover) with an increasing cover of herbaceous species, and a decreasing cover of graminoid species. Abundance of graminoids has earlier been connected to overgrowing and decrease in diversity in these grasslands (Pykälä 2005). Our results indicate that bryophyte-species turnover can depend also on the structure of vascular vegetation, not only on its biomass. Graminoid species with dense turfs in ground layer can have different competitive interactions with bryophytes than herbaceous species with more diverse growth forms.

The effects of grazing on life-strategy groups

The importance of competition and disturbances are intrinsic to the classification of bryophyte life strategies by During (1979, 1992). Hence, it can be predicted that colonists, in particular, should benefit from an increase of ground disturbances caused by grazing animals. Being effective in dispersal, colonists can quickly colonize patches of exposed mineral ground, enabling them to escape competition (During 1979, 1992, van Tooren *et al.* 1990). Perennials, on the other hand, can be expected to benefit especially from the decrease of competition by vascular plants. In our results, the effect of grazing on perennial species was almost identical to the effect on all bryophytes. The response of the colonists followed the same pattern although less uniformly as compared with the perennial group.

The results indicate that perennials and colonists benefit similarly from grazing at all measured scales because it decreases the vascular-plant biomass (competition) and increases the percentage of bare ground (ground disturbance).

There were, however, some signs of different responses of colonists and perennials to ground disturbances in our study. When we explored the microhabitat preferences of individual species, as compared with perennials many colonists clearly preferred microhabitats with more available bare ground, while vascular-plant height or litter cover had no effect (Fig. 1). Considering the classification criteria for the colonist group (During 1992), this result fits with both the suggested weak competition capability and effective dispersal capacity among the colonists. In general, for the colonists availability of suitable substrate is a more important determinant of survival than dispersal limitation (Miller & McDaniel 2004). Perennial bryophytes, however, are documented to be comparatively slow in colonizing pastures, even when source populations are found in immediate vicinity (van Tooren *et al.* 1990). In this study, there was always at least one other grazed pasture in the vicinity (< 200 m) of each study site and, hence, presumably a substantial regional species pool of colonists with airborne spores (Hutsemekers *et al.* 2008). Furthermore, many colonists were found even in the abandoned grasslands e.g. on sides of anthills (data not shown).

There were clear differences in the responses to grazing between perennial and colonist species even if the general positive effect of grazing was similar in both life-strategy groups. The results demonstrate that high bryophyte-species diversity in the intensively grazed grasslands results from the microhabitat heterogeneity that enables the persistent survival of species with different life strategies.

Conclusions

Our results demonstrate that perennial, colonist and occasional shuttle species form the basic bryophyte flora of the Finnish mesic semi-natural grasslands. We found a positive relationship between bryophyte-species richness and grazing

pressure with no apparent signs of significant negative effects of overgrazing. The results highlight the importance of grazing for biodiversity and conservation, and of competition and disturbance regimes for biodiversity in general. Even if there were apparent ecological differences among the moss species, bryophytes can be seen as one subordinate plant group when ecological processes are studied and management practices planned in productive habitats such as mesic grasslands. High bryophyte diversity can be expected in low-vegetation mesic grasslands subject to ground disturbance.

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