Effects of bryophyte removal and fertilization on established plants in a mountain grassland: changes of a fine-scale spatial pattern

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Bryophytes are can alter species composition in grassland communities, for example by affecting juvenile stages of grasses and other vascular plants, but their effect on spatial structure and on demography of established plants is less known. Therefore we studied effects of bryophytes on the spatial structure of a mountain grassland community using a bryophyte removal experiment, combined with fertilization. Spatial and temporal autocorrelations were measured using Moran I and tested with ANOVA. Fine-scale community response to removal was tested using redundancy analysis and a randomization test. Bryophyte removal affected patterns of spatial and temporal autocorrelations in some species and thus had an effect on the fine scale structure of the grassland. In particular, species with high ramet turnover (*Anthoxanthum alpinum* and *Deschampsia flexuosa*) responded positively to bryophyte removal in cells with high initial bryophyte density. In contrast to bryophyte removal, fertilization had no detectable effect on fine-scale spatial pattern, of either bryophytes or vascular plants. The removal experiment shows that bryophytes are not only passive gap-filling species, but that they may also actively contribute to formation of patches with lower ramet density of vascular plants.

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Bryophytes are capable of forming dense carpets. This has been attributed to positive interactions among bryophyte shoots, which overwhelm the effects of competition (van der Hoeven and During 1997, Bergamini et al. 2001, During and Lloret 2001, Pedersen et al. 2001). They also possess the capacity to close small gaps rapidly (Frego 1996, Økland 2000, Rydgren et al. 2001). If bryophytes co-occur in the same layer with vascular plants, such as grasses, fast spreading and formation of dense carpets may interfere with the growth of these plants. Fine-scale data on distribution of these two plant groups support this assumption (Wilson and Roxburgh 1994, Bergamini et al. 2001).

At a more mechanistic level, it has been repeatedly shown that bryophyte cover in grasslands affects juvenile stages of grasses and other vascular plants by changing predation, emergence and survival of seedlings (Keizer et al. 1985, Špačková et al. 1998, Kotorová and Lepš 1999, Zamfir 2000, Franzen 2001, Delach and Kimmerer 2002; reviewed by During and van Tooren 1990). This is likely to have profound effects on species whose dynamics are largely driven by seedling recruitment – in particular, dicotyledonous non-clonal plants. In contrast, the major species in grasslands, namely grasses, reproduce by seed only rarely (Zhukova and Ermakova 1985, Eriksson 1993) and are thus less prone to such effects. Observations

show that if bryophytes are present in a grassland, they are capable of altering both species composition and dominance structure of the community. In such cases they must interact with established plants and affect their ramet-level demography. Still the effect of bryophytes on demography of established plants is much less known relative to the wealth of information available on their effect on seedling recruitment.

The objective of this study is to identify the effects of bryophytes on spatial structure of a mountain grassland community. We hypothesize that in clonal plants such as grasses, processes affecting ramet-level demography should have some effect on the spatial pattern of the species. Therefore we performed an experiment where bryophytes were removed, and we compared change in spatial pattern of individual species at fine scales by means of spatial autocorrelation techniques. The experiment was performed under two levels of nutrient availability (fertilization) to identify whether increased productivity of grasses due to fertilization would alter the effect of bryophyte removal.

We concentrate on spatial patterns for two reasons. First, it has been often assumed in ecology that spatial patterns of species carry information about the processes that operate in the community. This reasoning, however widely used, is based on the assumption that different underlying processes would necessarily lead to different spatial patterns. While this relationship is far from universal (Lepš 1990, Dale 1999, Lepš et al. 1999), the information on spatial patterns can still be used to distinguish among alternative processes if spatial patterns produced by these competing alternatives are known either from theory or experience (Wilson 1995, Lepš et al. 1999). Second, in communities of plants that are short and of similar sizes (such as bryophytes or short-turf grasslands), there is little space for vertical differentiation; therefore most of the changes in dominance are due to horizontal replacement of moss carpets instead of overtopping as is commonly the case for vascular plants. Therefore spatial patterns may have direct bearing on dynamics of bryophyte communities (van Tooren and During 1988). The same applies, although to a lesser extent, also to short-turf grasslands such as those under study here. During showed that different types of temporal and spatio-temporal correlations are capable of revealing essential information about the mechanics of change (van Tooren et al. 1987, During and van Tooren 1988, van Tooren and During 1988). We therefore use spatial pattern as an indication of change in horizontal growth patterns after bryophytes have been removed.

Material and methods
Study site
The study site is located in a mountain grassland in the Krkonoše Mts., North Bohemia, Czech Republic (Severka settlement, ca 3 km NW of Pec pod Snǵ•kov, latitude 50º41′42″N, longitude 15º42′25″ E, altitude approx. 1100 m, NE facing slope of inclination 18º). This grassland was established several centuries ago. Traditional management was by mowing once a year and manuring once in several years. The experiment was done in a species-poor stand with prevailing *Nardus stricta* and *Deschampsia flexuosa* (association Sileno-Nardetum, alliance Nardo-Agrostion; the community classification follows Krahulec 1990). The grassland is species-poor with ca 6–10 species/50×50 cm and 2–4 species/3×3 cm (vascular plants). There are only four common grass species: *Anthoxanthum alpinum* Å. Löve et D. Löve, *Deschampsia flexuosa* (L.) Trin., *Festuca rubra* L. and *Nardus stricta* L. Other species of importance are *Polygonum bistorta* L., *Vaccinium myrtillus* L. and *Solidago virgaurea* L. Two bryophyte species are common, viz. *Pleurozium schreberi* (Brid.) Mitt. and *Rhytidiadelphus squarrosus* (Hedw.) Warnst. (Further reference to these species is by genus only.) In addition there are several uncommon species, i.e. vascular plants *Agrostis capillaris* L., *Campanula rotundifolia* L., *Deschampsia caespitosa* (L.) P.B., *Potentilla aurea* L., *Ranunculus acris* L. and *Silene dioica* (L.) Clairv. and bryophytes *Chiloscyphus profundus* (Nees) J. J. Engel et R.M. Schust., *Ditrichum cylindricum* (Hedw.) Grout, *Lophozia lycopodioides* (Wallr.) Cogn., *Plagiothecium cavifolium* (Brid.) Z. Iwats., *Pohlia* cf. *cruda* (Hedw.) Lindb. and *Ptilidium ciliare* (L.) Hampe. Nomenclature of bryophytes follows Váňa (1997).

Experimental design and data collection
Sixteen 50×50 cm plots were established in July 2000. The experiment used a two-way full factorial design, with two factors (bryophyte-removal and fertilization), each with two levels. Therefore four replicates were used for each factor-level combination. The plots were laid out in a systematic fashion but individual treatments were allocated to them randomly. In bryophyte-removal plots, all bryophytes (i.e. essentially *Pleurozium schreberi* and *Rhytidiadelphus squarrosus*) were carefully removed by forceps in autumn 2000. In the no-bryophyte-removal plots, bryophytes were left intact. Bryophyte removal was repeated always in spring (May) and in autumn (September) in order to suppress regrowth. Fertilized plots received the following amounts of nutrients: N: 5g m^{-2}, P: 2.5g m^{-2}, K: 2.5g m^{-2}, Mg: 2.5g m^{-2}, Ca: 2.5g m^{-2} (as NH_4Cl, $NaNO_3$, Na_2HPO_4, KCl, $MgCl_2$, $CaCl_2$). This amount was ap-

plied three times during the growth season: in early spring after snowmelt (May), in summer (July) and in September, always diluted in 2 l of water. Non-fertilized plots received equal amounts of water. Plots were fertilized both in 2001 and 2002.

The vegetation recording started in July 2000 before the treatments started. A 5×5 cm grid of cell was laid over each plot and cover of each species was visually estimated using a five-point scale (cover less than 2%, 2–25%, 25–50%, 50–75%, 75–100%) for each cell separately. For the data analyses these values were recoded into the mean values of each category.

Data analysis

First, spatial autocorrelations of individual species cover (Moran I; Upton and Fingleton 1985) were computed for each recording of each plot. Moran I measures correlation of values of a single variable (species cover in this case) at two different spatial locations (cells) that are separated by a fixed distance (lag). The resulting value is a function of this distance. Two spatial lags were used: 1 cell (adjacent cells compared) and 2 cells (cells separated by exactly one other cell). The Moran I values were analyzed at the plot level. Values of each recording were taken as the response variable at the plot level and analyzed by means of analysis of variance, with bryophyte removal and fertilization as between-subject factors (defined at the level of plots), and time and lag as within-subject factors (defined at the level of individual recordings). Seven species of vascular plants were analyzed: *Anthoxanthum, Deschampsia*, *Festuca*, *Nardus, Polygonum, Vaccinium* and *Solidago,* together with two species of bryophytes, *Pleurozium* and *Rhytidiadelphus.* Furthermore, Moran I's for temporal autocorrelation were calculated in a similar fashion for each set of recordings of each plot. Temporal autocorrelation coefficients were also analysed by means of analysis of variance. If several coefficients of different lags were calculated from one plot, tests were done using repeated measurements ANOVA in order to prevent inflation of the error df. All ANOVAs were performed using S-Plus 2000 (Mathsoft 2000).

Effects of bryophyte removal on vascular plants at the cell level were tested using a linear multivariate technique, redundancy analysis (RDA, ter Braak and Šmilauer 1998). Redundancy analysis is an extension of principal components analysis that enables identification of gradients in species composition under the constraint that they are correlated with a separate set of independent (environmental) variables. A linear technique was justified since the gradient lengths in the data were sufficiently short. RDA was used to test whether treated (bryophyte removal) and untreated plots differ in the correlation between initial bryophyte
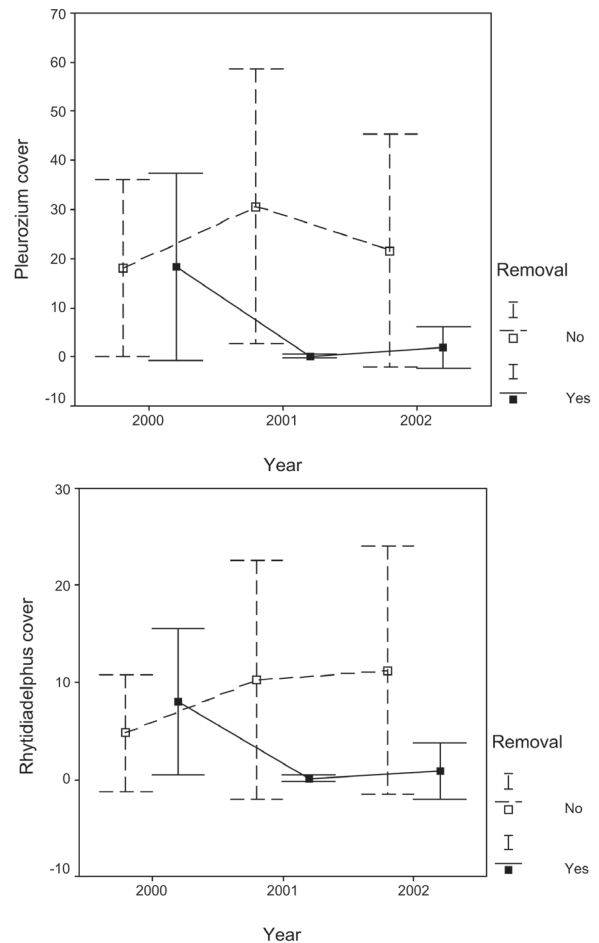

Fig. 1. Change in mean cover per 5×5 cm cell of *Pleurozium schreberi* (a) and *Rhytidiadelphus squarrosus* (b) in July. Bars indicate ± SD. Removal began in autumn 2000. Fertilized and non-fertilized plots are pooled.

cover at the level of 5×5 cm cells and their floristic composition throughout the experiment. Floristic composition was taken as dependent (species) data. Cell ID's, time, initial bryophyte cover, time×initial bryophyte cover and time×treatment (bryophyte removal) were used as covariates. These remove variability that should be attributed to sources independent of the treatments used. The triple interaction of time×initial bryophyte cover×treatment (bryophyte removal) was taken as a tested independent (environmental) variable. Fertilization levels were pooled for this analysis. The analysis was done in the program CANOCO ver. 4.5 (ter Braak and Šmilauer 1998). To show different projections of the data, four different types of RDA were used (Tab. 3) by combining standardization by species and cover transformation. Standardization by species gives greater weight to rare species,
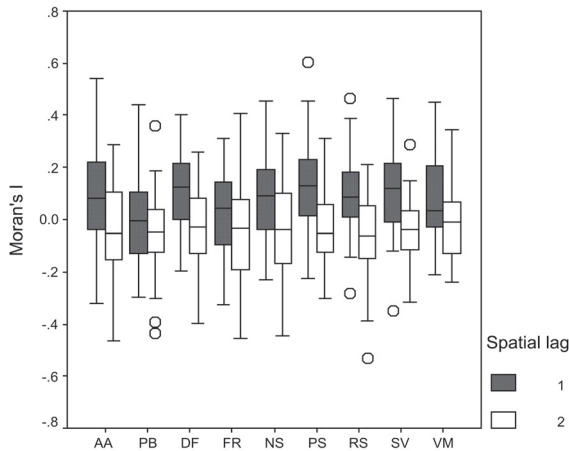
Fig. 2. Spatial autocorrelation over lags of one and two cells (5×5 cm in size) in summer recordings (Moran's I) of the major species in the grassland. AA, *Anthoxanthum alpinum*, PB, *Polygonum bistorta*, DF, *Deschampsia flexuosa*, FR, *Festuca rubra*, NS *Nardus stricta*, PS *Pleurozium schreberi*, RS, *Rhytidiadelphus squarrosus*, SV *Solidago virgaurea*, VM *Vaccinium myrtillus.* All treatments are pooled.

while square-root transformation gives more weight to differences in small cover values. In order to calculate the probability of Type I error the data-set was randomised by (i) full randomization of whole plots (cells kept together) and (ii) randomization of cells within whole plots by rotation, reflexion and positional shift on the toroidal plane. Since this requires a double split-plot randomization which is unavailable in CANOCO, a special randomization program was written to randomize the data (Herben et al. 2003). 200 permutations were done.

Results

Moss removal reduced the cover of the two initially dominant species, *Pleurozium schreberi* and *Rhytidiadelphus squarrosus*, to about 1/10 of their cover before the removal (Fig. 1). However, there was no further decrease in their cover during the period of removal. The cover in 2002 was similar to that in 2001, indicating that cover in summer was the result of moss re-growth after removal.

Species present in the grasslands differed markedly in their patterns of spatial autocorrelations at short spatial lags (Fig. 2). The dominant mosses ranked first and third highest Moran I over lag 1 among the all species; there was no major difference among species when a lag of 2 cells was used.

Spatial patterns of the vascular plants changed as the result of bryophyte removal only in some species (Table 1). The important indicator of response, i.e. time×removal interaction was significantly different from zero for *Festuca*, *Solidago* and *Vaccinium*. The responses of other species were not significant. In all three species, intensity of the spatial patterns (i.e. magnitude of the Moran I over spatial lag of 1) increased as the result of moss removal albeit already in the first year in *Festuca* and only in the second year in *Vaccinium* and *Solidago*. Surprisingly, the spatial pattern of neither dominant moss changed as the result of either removal or fertilization. Fertilization had no detectable effect on spatial pattern of either vascular plants or bryophytes.

Both removal and fertilization also affected patterns of temporal autocorrelations in some species (*Festuca, Solidago* and *Polygonum*, Table 2); effects were significant only at the level of interaction between temporal lag and treatment (either removal or fertiliza-

Table 1. Analysis of variance of the spatial structure of the plots, expressed by means of Moran I, with removal and fertilization as main factors, and time and lag as within-subject factors. Values in the table are F- statistics (only values significant at alpha = 0.1 are shown). *, P<0.05; **, P<0.01; ***, P<0.001.

Effect	df	*Nardus*	*Deschampsia*	*Anthoxanthum*	*Festuca*	*Solidago*	*Polygonum*
Removal	1,12						
Fert	1,12						
Removal×Fert	1,12						
Time	2, 63						
Lag	1, 63	13.2***	24.4***	12.3***	6.0***	43.3***	12.7***
Lag×Removal	1, 63						4.2*
Lag×Fert	1, 63						
Time×Lag	2, 63		3.3*				
Time×Removal	2, 63				3.3*	4.9*	5.7**
Time×Fert	2, 63						
Time×Lag×Removal	2, 63						
Time×Lag×Fert	2, 63						
Time×Removal×Fert	2, 63						

Table 2. Analysis of variance of the temporal autocorrelations of species (Moran I), with removal and fertilization as main factors, and temporal lag as within-subject factor. Values in the table are F- statistics (only values significant at alpha = 0.1 are shown). +, $P<0.1$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Effect	df	*Nardus*	*Deschampsia*	*Anthoxanthum*	*Festuca*	*Solidago*	*Polygonum*
Vaccinium							
Removal	1,12						
Fert	1,12						
Removal×Fert	1,12						
TempLag	1, 29	42.7***	6.6*			16.7***	48.0***
TempLag×Fert	1, 29				3.4+	5.8*	6.1*
TempLag×Removal	1, 29	3.6+			6.9*	5.2*	4.3*

tion). In *Festuca*, removal resulted in very stable patches (temporal autocorrelation over two years even exceeded, albeit insignificantly, the mean value of that over one year), whereas the other two species responded in the reverse fashion so that in the removal plots the Moran I over one year was higher. No significant effect of any treatment was found for spatial lag over two years. Fertilization affected spatial patterns of two dicot species, *Solidago* and *Polygonum*; in both species, temporal autocorrelation over one year was lower in fertilized plots.

Fertilization did not affect spatial pattern of *Rhytidiadelphus* or *Pleurozium* (if non-removal plots only were analysed). Temporal pattern was affected only in *Pleurozium* (lag×fertilization: F = 6.98, df = 1,14, P = 0.019), which showed a steeper decrease in Moran I (higher turnover) at non-fertilized plots.

Multivariate tests showed that moss removal affected fine-scale species composition differently at cells with high initial bryophyte cover, although the effect was not very strong and was significant only for the correlation matrix of square root-transformed cover values (Table 3). In particular, *Anthoxanthum* and *Deschampsia* (and to a lesser extent *Solidago* and *Vaccinium*) were stimulated by bryophyte removal in bryophyte-rich plots relative to bryophyte-poor plots (Table 4). *Festuca* and *Polygonum* were weakly negatively affected.

Discussion

The results reported here show that bryophyte removal affected the fine-scale spatial structure of the grassland. This indicates that bryophytes affect the grassland species composition by (very) local interactions, changing local demography of grasses in bryophyte-rich patches. This is also supported by the fact that the cell-level test showed that bryophyte removal affected remaining grasses differently depending on the initial cover of bryophytes in the cells. It is likely that the major component of the effect is mediated through ramet-level demography, as seedling establishment is a rather rare event in this grassland (Suzuki et al. 1999). In particular, species with high ramet turnover and loose tussocks (*Anthoxanthum* and *Deschampsia*; Law et al. 1997) responded strongly positively if the cells were emptied by the bryophyte removal. Species with dense tussocks (*Festuca, Nardus*, and all dicots) responded much less. Still there is no significant correlation between fine-scale species composition of vascular plants and bryophytes in the year before the experiment began (Wagnerová 2003); this contrasts with findings from other grassland systems (Wilson and Roxburgh 1994, Ingerpuu et al. 1998).

In contrast to bryophyte removal, fertilization had little effect on spatial pattern of either bryophytes or vascular plants. The low doses of fertilizer do not entirely account for the lack of effect on bryophytes, as the same levels had a significant effect on biomass

Table 3. Multivariate tests whether bryophyte removal affected species composition differently in bryophyte-rich and bryophyte-poor cells. For more details on the analysis, see Methods.

Analysis	Standardization by species	Cover transformation	% variability explained by the interaction	P
No. 1	no	none	0.4	0.165
No. 2	no	square root	0.4	0.075
No. 3	yes	none	0.3	0.170
No. 4	yes	square root	0.5	0.045

Table 4. Scores of individual at the first canonical axis in the analysis No. 4. Positive values mean that the species increased in the removal treatment in the cells which initially had high bryophyte cover.

Species	Score at the 1st canonical axis
Nardus	–0.0099
Deschampsia	0.0617
Anthoxanthum	0.0743
Festuca	–0.0214
Solidago	0.0250
Polygonum	–0.0230
Vaccinium	0.0240

and species composition of vascular plants at the larger scale (plot-level, Wagnerová 2003). Other experiments have shown that bryophytes are affected also by competition from vascular plants (Bergamini and Peintinger 2002), which is likely to become more intense if the vascular plant biomass rises. The absence of a fine-scale effect thus indicates that the fertilization affects all ramets (or patches) approximately at the same rate. In contrast, the effect of bryophytes (and hence of their removal) in the grassland is much more local, and affects fates of individual ramets differentially depending on their position, either relative to other ramets or to bryophyte-rich patches. With the doses we used, we conclude that there was no significant interaction between the effect of fertilization and bryophyte removal on the spatial pattern; growth enhancement by fertilization did not enable the vascular plants to cope better with the (putatively competitive) effect of the bryophytes.

In general, it should be noted that ecological roles of bryophytes in grasslands still awaits deeper study. While bryophytes occur in many different types of grasslands, ranging from *Carex*-rich wet meadows to dry "steppe" grasslands, very little general information on the role of bryophytes (apart from the interaction with germination and seedlings) is known. Still they are clearly capable of interfering with the growth and ramet demography of established grasses, and thus able to affect structure, productivity and species richness of vascular plants. In many cases, a change of focus is needed. Bryophytes are not necessarily only passive gap-filling species, but contribute to building the system in a manner that can be studied using approaches similar to those used, for example, in peat bogs (Malmer et al. 1994).

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