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SPECIES RICHNESS OF VASCULAR PLANTS, BRYOPHYTES AND LICHENS IN DRY GRASSLANDS: THE EFFECTS OF ENVIRONMENT, LANDSCAPE STRUCTURE AND COMPETITION

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Abstract: We studied the relative importance of local habitat conditions and landscape structure for species richness of vascular plants, bryophytes and lichens in dry grasslands on the Baltic island of Öland (Sweden). In addition, we tested whether relationships between species richness and vegetation cover indicate that competition within and between the studied taxonomic groups is important. We recorded species numbers of vascular plants, bryophytes and lichens in 4 m^2 plots ($n = 452$), distributed over dry grassland patches differing in size and degree of isolation. Structural and environmental data were collected for each plot. We tested effects of local environmental conditions, landscape structure and vegetation cover on species richness using generalized linear mixed models. Different environmental variables explained species richness of vascular plants, bryophytes and lichens. Environmental effects, particularly soil pH, were more important than landscape structure. Interaction effects of soil pH with other environmental variables were significant in vascular plants. Plot heterogeneity enhanced species richness. Size and degree of isolation of dry grassland patches significantly affected bryophyte and lichen species richness, but not that of vascular plants. We observed negative relationships between bryophyte and lichen species richness and the cover of vascular plants. To conclude, effects of single environmental variables on species richness depend both on the taxonomic group and on the combination of environmental factors on a whole. Dispersal limitation in bryophytes and lichens confined to dry grasslands may be more common than is often assumed. Our study further suggests that competition between vascular plants and cryptogams is rather asymmetric.

Keywords: Alvar, Biodiversity, Dispersal limitation, Environmental heterogeneity, Fragmentation, Soil pH, Spatial autocorrelation

INTRODUCTION

Identifying the processes that determine species diversity remains a challenge in ecological research (GRACE 1999, TILMAN 2000, LOREAU et al. 2001). Numerous studies on small spatial scales show that habitat quality plays an important role for plant species richness, with soil properties and light being the most commonly studied environmental factors (compare review by GRACE 1999). Besides habitat quality, landscape structure and history are considered as important factors for species richness and species occurrence probabilities. The distribution of many species in the current landscape largely reflects historical land-use

(BRUUN et al. 2001, COUSINS & ERIKSSON 2001, ERIKSSON et al. 2002). Biodiversity and metapopulation theory further predicts that the smaller and more isolated habitat patches are, the fewer species they contain (ROSENZWEIG 1995, HANSKI 1999). This is explained by larger extinction risks of local populations due to smaller local population sizes with decreasing patch size, and lower rates of colonization as an effect of isolation (HANSKI 1999). The species pool hypothesis suggests that such a smaller regional species pool results in a lower small-scale species density (ZOBEL 1992, PÄRTEL 2002). Whereas some studies in dry grasslands confirmed this (PÄRTEL et al. 1996, PÄRTEL & ZOBEL 1999) others failed to do so (KRAUSS et al. 2004). Additionally, the relative importance of habitat quality and landscape structure has seldom been quantified (DUPRÉ et al. 2002, KOLB & DIEKMANN 2004).

Interspecific competition is among the most frequently discussed local processes determining species richness (GRACE 1999). The “hump-back” shape of the relationship between species richness and productivity (commonly quantified by the biomass or vegetation cover) and/or disturbance is a well-established “law” in community ecology (GRIME 1979, HOUSTON 1979, GRACE 1999, WAIDE et al. 1999). Several authors suggest that interspecific competition reduces species richness in productive habitats (GRIME 1979, GRACE 1999), but in nutrient-poor environments this may be quite unimportant (PÄRTEL et al. 2000).

So far, most research has focused on vascular plants, whereas few papers have examined the processes determining species richness of bryophytes and lichens (“cryptogams”). Bryophyte, lichen and vascular plant species richness have been shown to respond differently to some environmental factors (PAUSAS 1994, INGERPUU et al. 1998, 2003), but in the same way to others (INGERPUU et al. 1998, GOULD & WALKER 1999). Some authors found close correlations between cryptogam and vascular plant species richness (ZAMFIR et al. 1999, INGERPUU et al. 1998), whereas others failed to do so (HERBEN 1987, PHARO et al. 1999). Regional patterns of bryophyte and lichen species richness have rarely been considered. In general, bryophytes and lichens have distinctly larger distribution ranges and smaller diaspores than vascular plants and thus dispersal limitation may be less common.

Most studies deal with bryophytes and lichens that inhabit special micro-sites such as tree trunks, logs or boulders (e.g. GUSTAFSSON & ERIKSSON 1995, WEIBULL & RYDIN 2005). In many vegetation types, however, vascular plants, bryophytes and lichens all form a substantial part of the plant species assembly (ZAMFIR et al. 1999, INGERPUU et al. 2003). It is often suggested that competition between vascular and non-vascular plants is strongly asymmetric (e.g. INGERPUU et al. 2003), but empirical evidence for this is scarce and somewhat controversial. Some studies showed that a dense cryptogam layer may inhibit regeneration of vascular plants (DURING & VAN TOOREN 1990, VAN TOOREN 1990, ZAMFIR 2000). In general, little is known about interspecific competition among bryophytes and lichens (DURING & VAN TOOREN 1990, RYDIN 1997).

We studied small-scale species richness patterns of vascular plants, bryophytes and lichens in dry grasslands on the Swedish island of Öland in the Baltic Sea (Fig. 1). The island contains the most extensive dry grasslands in Scandinavia. Furthermore, calcareous grasslands, especially those of the Great Alvar on Öland, are known for their exceptionally high species

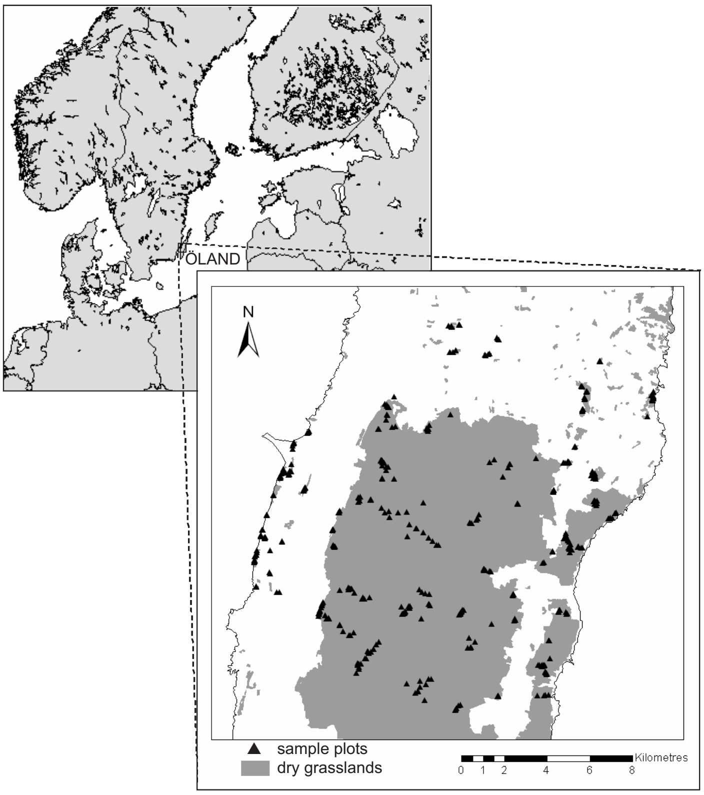


Fig. 1. Investigation area with locations of all sample plots and the distribution of dry grasslands in the northern part of southern Öland.

richness, both on a local and regional scale (ROSÉN 1982, PÄRTEL & ZOBEL 1999, DENGLER 2005). Cryptogams form a substantial part of the species assemblage of many dry grassland types (DENGLER & LÖBEL 2006). Dry grasslands on Öland have been used as model systems for biodiversity research by many authors (e.g. VAN DER MAAREL & SYKES 1993, HUBER 1999, ZAMFIR et al. 1999). Studies, however, are mainly performed on the huge contiguous dry grassland area of the Great Alvar, often within a single plant community type. In our study, we considered all dry grassland types of southern Öland, including those occurring both on, and outside, the Great Alvar. By doing so, we included much longer environmental gradients than previous studies, as well as dry grassland patches of very different sizes and degrees of isolation.

By investigating fine-scale plant species richness patterns in this study system, we aim to test (1) the relative importance of local habitat conditions and landscape structure on species richness, (2) whether vascular plant, bryophyte and lichen species richness are related to these factors in different ways, and (3) whether relationships between species richness and vegetation cover suggest that interspecific competition within and between these taxonomic groups is important.

MATERIAL AND METHODS

Study area

Our study area comprises the northern part of southern Öland (Fig. 1). The climate of Öland shows both continental and oceanic traits. While the temperature regime is rather oceanic, the annual precipitation is comparatively low, with especially low values in summer (SJÖRS 1999). The solid geology comprises sedimentary rocks of Cambrian and Ordovician age. In most parts of the island, however, the bedrock is covered by Quaternary deposits, although in the southern part, where the Great Alvar is located, these are thin or missing. Lime-poor moraine soils intermix with weathered soils of varying thickness. Compared with other limestone in northern Europe, the Ordovician limestone on Öland is hard with horizontal layers (KRAHULEC et al. 1986, STERNER & LUNDQVIST 1986). In some places these soils are poorly drained and thus often strongly affected by frost in winter. Glacifluvial deposits form sandy soils along the Ölandic west coast and in the northeastern part of the study area (STERNER & LUNDQUIST 1986). Dry grassland patches of varying size and degree of isolation (Fig. 1) occur on all described soil types.

The island was first colonized by humans during the early Stone Age (ROSÉN 1982, ALM KÜBLER 2001), and the current thin soils of the Great Alvar are probably the result of soil erosion due to intensive grazing during the Bronze and Iron Ages, and the early Medieval phase (DIERßEN 1996). Grazing, small-scale agriculture, and fire-wood cutting over many centuries has effectively kept shrub- and woodland back (KRAHULEC et al. 1986). In contrast to this unique land-use history, many dry grasslands outside the great Alvar occur on former fields, close to road-verges or villages and in recreation areas. These are partly mown or unused.

The sampled dry grassland types belong to the phytosociological classes *Festuco-Brometea* BR.-BL. & TX. ex KLIKA & HADAČ 1944 (semi-dry basiphilous grasslands) and *Koelerio-Corynephoretea* KLIKA in KLIKA & V. NOVÁK 1941, including the *Sedo-Scleranthenea* (BR.-BL. 1955) DENGLER in DENGLER et al. 2003 (weathered rock and outcrop communities) and the *Koelerio-Corynephorenea* (KLIKA in KLIKA & NOVÁK 1941) DENGLER in DENGLER et al. 2003 (dry grasslands on sandy soils). Altogether, 15 associations (or equivalent units) could be distinguished and were sampled (LÖBEL 2002, DENGLER & LÖBEL 2006).

Data collection

During the spring and summer 2001, we recorded the presence of all vascular plant, bryophyte and lichen species (with the exception of epilithic crustose lichens) in 452 sample plots of 2 m × 2 m. For the purposes of this study, we generally accepted infraspecific taxa as species. Critical specimens were collected and identified using microscopy. Sample plots were distributed throughout the whole investigation area and their exact positions determined with a GPS (Garmin eTrex, ± 5 m) (Fig. 1). We tried to select samples that represented the whole variation of community types and sizes of dry grassland patches.

Soil depth (cm, measured with a pointed iron rod, mean value of five randomly chosen positions), microtopography (cm, maximum height difference within the plot measured with a ruler), cover of bare rock (%), and the total and group-specific cover of vegetation (%) were determined in the field. In addition, we noted whether the site was grazed, mown or not used at all; if the management regime was not obvious in the field, we got information about the management regime from a local expert (E. Rosén). We took a mixed soil sample of the uppermost layer (0–10 cm) at different points of each plot. The samples were dried at 105 °C and their pH (in distilled water) was measured.

We determined the size of all sampled dry grassland patches and the spatial isolation of sample plots by digitizing all dry grasslands within the investigation area from a detailed vegetation map (METRIA 2000) in a geographical information system (ArcGis 9.0) (Fig. 1). We thoroughly checked the descriptions of all vegetation types delimited on the vegetation map (METRIA 2000) before deciding which stands constitute dry grassland patches in our sense. We chose the proportion of dry grasslands within a circle of the radius r around the respective sample plot as an inverse isolation measure. We tested five different radii, $r = 100$ m, 250 m, 500 m, 1 km and 2.5 km. We also considered other isolation measures, e.g. the edge-to-edge distance to the nearest different dry grassland patch and the connectivity index (HANSKI 1999), combining the distance to, and the size of surrounding dry grassland patches. These, however, were problematic given the large differences in size of the sampled dry grassland patches and the large number of plots which were located on the Great Alvar.

Statistical analysis

Local environmental variables, dry grassland patch size and isolation

We tested the effects of the local environmental variables on patterns of total species richness and species richness of the different taxonomic groups by fitting generalized linear mixed models (GLMM) with a Poisson error distribution and a log-link function. We applied a function (glmmPQL in the MASS library; VENABLES & RIPLEY 1999) that uses penalized quasi-likelihood for parameter estimation, and therefore, F-tests were applied for significance tests. The local environmental variables were treated as fixed factors, while the dry grassland patch within which a sample plot was located constituted a random factor. To account for spatial autocorrelation, we tested whether inclusion of an exponential spatial correlation structure (PINHEIRO & BATES 2000) for the within-group errors gave a better fit than the independent errors model.

Multiple starting models were built using the local environmental variables as predictors. We included two-way interactions and squared terms of continuous variables to account for non-linearities. The models were simplified by manual backward elimination until only significant terms were left; the criterion for inclusion was $P = 0.05$ in F-tests. We then extended the described models. We tested whether the size (ha) or degree of isolation of the dry grassland patch within which a sample plot was located significantly improved the model. We also tested the interaction among these two variables. The significance of the spatial autocorrelation structure was assessed using likelihood ratio tests (AZZALINI 1996).

Biotic interaction effects

We used different approaches to assess the effects of interspecific competition on species richness. First, we related species richness to the total vegetation cover, to the cover of the different taxonomic groups, and to the species richness of the respective other taxonomic

Table 1. Means, medians, standard deviations (s.d.), minima and maxima of species numbers (per 4 m^2 plot), vegetation cover degrees, and the independent variables.

Variable	Mean	s.d.	Median	Minimum	Maximum
Total species number	40.4	13.6	39	7	80
Number of vascular plants	23.6	8.2	24	4	49
Number of bryophytes	11.4	8.8	8	0	40
Number of lichens	5.4	5.3	4	0	24
Total vegetation cover (%)	81.9	20.1	90	15	100
Cover vascular plants (%)	69.1	23.6	75	4	100
Cover bryophytes (%)	32.1	19.8	30	0	85
Cover lichens (%)	10.9	14.2	5	0	75
Soil pH	6.3	1.2	6.5	3.5	8.1
Soil depth (cm)	17.6	16.7	12	0	60
Cover bare rock (%)	3.6	10.6	0	0	80
Microtopography (cm)	2.0	4.2	0	0	30
Size of dry grassland patch (ha)	6 989	6 661	13 550	0.05	13 550
Proportion of dry grasslands within 500 m distance (%)	59.3	38.8	46.6	0.3	100.0

groups by fitting GLMM in the same way as described above. We tested whether adding a squared term significantly improved the models. Since these relationships may mirror differences in habitat requirements among the taxonomic groups rather than competition effects, we further modelled the residuals of the GLMM (with the local environmental variables and dry grassland patch size and isolation as predictors) as a function of vegetation cover and species richness of the respective other taxonomic groups. In that way, we tested whether the vegetation cover explains further variation in species richness that could not be assigned to environmental effects. In this case, we used GLMM with a Gaussian error structure and an identity link because our response variables (residuals) were continuous. The spatial correlation structure was modelled as before.

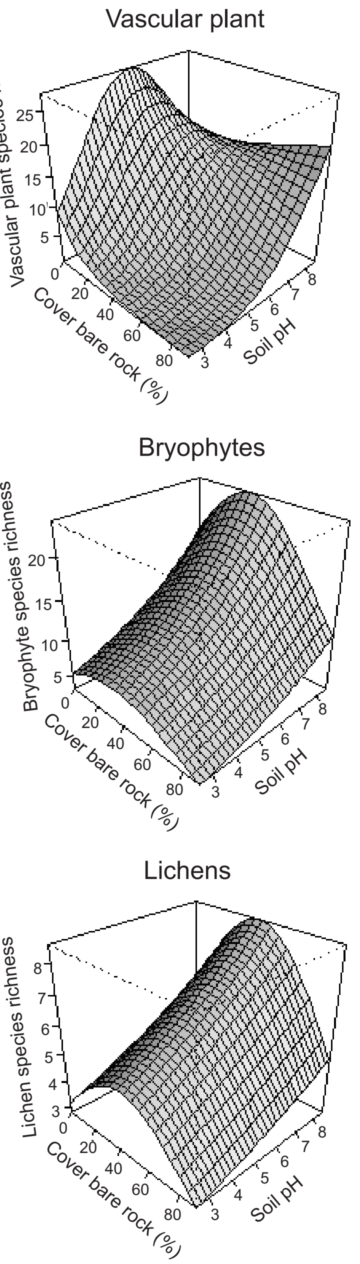
We used the free software R 1.8.1 (R Development Core Team 2004) with the add-on libraries geoR version 1.4-5 (Ribeiro Jr. & Diggle 2001) and MASS version 7.1-13 (Venables & Ripley 1999) for the statistical analyses.

RESULTS

We recorded a total of 300 vascular plant, 153 bryophyte and 84 lichen species. Means, standard deviations and ranges of the species numbers per plot (4 m^2) and of the independent variables are given in Table 1. Out of the total 452 plots, 341 were grazed, 23 mown, 72 not used, and 16 road-side.

Local environmental variables

Species richness of all three taxonomic groups was best predicted by the soil pH (Table 2). Whereas bryophyte and lichen species richness linearly increased with increasing pH, the squared term (negative sign) explained most variation in vascular plant species richness



Vascular plant

Bryophytes

Lichens

Fig. 2. Effects of soil pH and cover of bare rock (%) on vascular plant, bryophyte, and lichen species richness. Response surfaces are calculated based on the partial regression coefficients of the fitted GLMM with the local environmental variables and dry grassland patch size and degree of isolation as predictors.

(Fig. 2). Bryophyte and lichen species richness increased with decreasing soil depth, but slightly decreased again on extremely shallow soils. Vascular plant species richness was negatively affected by the cover of bare rock, whereas bryophyte and lichen species richness showed a unimodal response. Microtopography enhanced species richness of vascular plants and bryophytes. In contrast, lichen species richness was highest at intermediate levels of microtopography. Interaction effects of soil pH with the cover of bare rock and microtopography were significant in vascular plants, but not in bryophytes and lichens (Fig. 2). The type of management regime was not significant and therefore not included in any of the models. Total species richness was mainly explained by the same variables as bryophyte and lichen species richness.

Dry grassland patch size and degree of isolation, spatial autocorrelation

The size of the dry grassland patch within which a sample plot was located significantly enhanced total, bryophyte, and lichen species richness (Table 2). In contrast, it was not important for vascular plant species richness. Total and lichen species richness further increased with the proportion of dry grasslands within a circle around the sample plot; the best fit was given for a circle with the radius r = 500 m. Species richness of all tested taxonomic groups showed spatial autocorrelation.

Relationships between species richness patterns and vegetation cover

For vascular plants, species richness linearly increased with cover of vascular plants (Fig. 3). However, when using residuals of the GLMM of vascular plant species richness as a response variable, a slight decrease at high cover was visible (Table 3). The relationship between

Table 2. Generalized linear mixed models with a Poisson error distribution and a log-link function for species richness of all plants and species richness of vascular plants, bryophytes, and lichens on 4 m^2. Coefficient signs, F-statistics and P-values are given for the fixed factors. Only significant variables ($P < 0.05$) were included in the models; variables not included in the respective model are reported as non significant (n.s.). The dry grassland patch within which a sample plot was located constituted a random factor. In addition, likelihood-ratio tests of including an exponential spatial correlation structure for the within-group errors are presented. The range parameter indicates the distance in metres up to which the response variable shows autocorrelation. The total number of observations was $n = 452$, the number of independent groups was $n_G = 107$.

	Total plant species richness			Vascular plant species richness			Bryophyte species richness			Lichen species richness		
Exponential spatial correlation structure	range = 51.1, $\chi^2 = 54.6$, $P < 0.001$			range = 197.0, $\chi^2 = 110.5$, $P < 0.001$			range = 11.2, $\chi^2 = 47.8$, $P < 0.001$			range = 114.2, $\chi^2 = 71.8$, $P < 0.001$		
Variable	Sign	F	P	Sign	F	P	Sign	F	P	Sign	F	P
Soil pH	+	84.3	<0.001	+	40.6	<0.001	+	217.8	<0.001	+	72.6	<0.001
(Soil pH)^2		n.s.		-	93.9	<0.001		n.s.			n.s.	
Soil depth	-	13.0	0.001		n.s.		-	39.2	<0.001	-	13.8	<0.001
(Soil depth)^2	+	9.8	0.002		n.s.		+	27.6	<0.001	+	26.8	<0.001
Cover bare rock	+	0.2	0.691	-	20.7	<0.001	+	2.2	0.140	+	5.1	0.017
(Cover bare rock)^2	-	9.2	0.003		n.s.		-	9.0	0.003	-	6.4	0.012
Microtopography	+	13.3	<0.001	+	8.8	0.004	+	20.6	<0.001	-	1.7	0.190
(Microtopography)^2		n.s.			n.s.			n.s.		+	11.6	0.001
Soil pH × Cover bare rock		n.s.		+	13.0	<0.001		n.s.			n.s.	
Soil pH × Microtopography	-	9.2	0.003	-	8.6	0.004	n.s.	n.s.				
Size of dry grassland patch	+	20.0	<0.001		n.s.		+	15.6	<0.001	+	31.8	<0.001
Proportion of dry grasslands within 500 m distance	+	15.2	<0.001		n.s.			n.s.		+	15.5	<0.001

Table 3. Generalized linear mixed models predicting species richness and residuals of the generalized mixed linear models with the environmental variables and landscape structure as predictors as a function of vegetation cover, respectively. Vegetation cover variables were treated as fixed factors and tested one by one separately. Coefficient signs, *F*-statistics and *P*-values are presented. The dry grassland patch within which a sample plot was located constituted a random factor. Models included an exponential spatial correlation structure for the within-group errors. The total number of observations was $n = 452$, the number of independent groups was $n_G = 107$.

Variable	Species richness			Residuals GLMM		
	Sign	*F*	*P*	Sign	*F*	*P*
Total plant species richness						
Total vegetation cover	+	4.5	0.034	+	23.3	< 0.001
(Total vegetation cover)^2	-	17.2	< 0.001	-	3.9	0.048
Vascular plant species richness						
Cover vascular plants	+	157.2	< 0.001	+	33.3	< 0.001
(Cover vascular plants)^2		n.s.		-	5.0	0.026
Cover bryophytes	+	9.2	0.003		n.s.	
(Cover bryophytes)^2	-	5.6	0.019		n.s.	
Cover lichens	+	5.9	0.015	+	4.2	0.040
(Cover lichens)^2		n.s.			n.s.	
Species richness bryophytes	-	12.2	< 0.001		n.s.	
Species richness lichens	-	8.2	0.003		n.s.	
Bryophyte species richness						
Cover bryophytes	+	6.6	0.010	+	4.4	0.038
(Cover bryophytes)^2	-	4.6	0.033	-	3.4	0.064
Cover vascular plants	-	82.4	< 0.001		n.s.	
(Cover vascular plants)^2		n.s.			n.s.	
Cover lichens	+	7.9	0.005	+	8.0	0.005
(Cover lichens)^2	-	18.6	0.001	-	12.2	< 0.001
Species richness vascular plants	-	10.0	0.002	+	6.5	0.011
Species richness lichens	+	192.7	< 0.001	+	27.7	< 0.001
Lichen species richness						
Cover lichens	+	189.1	< 0.001	+	252.1	< 0.001
(Cover lichens)^2	-	79.9	< 0.001	-	42.8	< 0.001
Cover vascular plants	-	131.5	< 0.001	+	13.6	< 0.001
(Cover vascular plants)^2	-	5.1	0.024	-	25.1	< 0.001
Cover bryophytes	+	6.2	0.013	+	1.1	0.287
(Cover bryophytes)^2	-	16.8	< 0.001	-	9.5	0.002
Species richness vascular plants	-	6.6	0.011		n.s.	
Species richness bryophytes	+	190.1	< 0.001	+	16.7	< 0.001

vascular plant species richness and bryophyte cover was unimodal, but we did not observe any relationships between the residuals of the GLMM of vascular plant species richness and bryophyte cover. In contrast, we observed a positive relationship between vascular plant species richness and lichen cover in both models. Vascular plant species richness was negatively related to bryophyte and lichen species richness, but when using residuals of the GLMM of vascular plant species richness as a response variable, we did not observe any relationships.

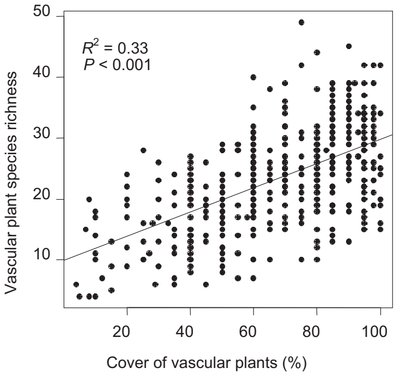


Fig. 3. Relationship of vascular plant species richness on 4 m^2 with the cover of vascular plants.

We observed a unimodal relationship between bryophyte species richness and bryophyte cover. Bryophyte species richness was negatively related to the cover of vascular plants, but residuals of the GLMM of bryophytes species richness were not related to the latter (Fig. 4). Bryophyte species richness showed a unimodal response to lichen cover in both models. Bryophyte species richness was negatively related to species richness of vascular plants. In contrast, residuals of the GLMM of bryophyte species richness were positively related to the latter. Both bryophyte species richness and residuals of the GLMM were positively related to lichen species richness.

We observed a unimodal relationship between lichen species richness and lichen cover. Lichen species richness was negatively related to the cover of vascular plants, but residuals of the GLMM of lichen species richness showed a unimodal response. However, the negative effect of the squared term was still strong compared to the positive effect of the linear term. The same was true for the unimodal relationship between lichen species richness and bryophyte cover. Lichen species richness was negatively related to vascular plant species richness, but positively to that of bryophytes.

DISCUSSION

Local environmental conditions

Our results suggest differences in habitat requirements between vascular plants and cryptogams. The effects of habitat quality on species richness were strong compared with those of landscape structure. This confirms the hypothesis of DUPRÉ & EHRLÉN (2002) that with an increasing environmental gradient among sampling units, habitat quality is likely to increase, whereas habitat configuration is likely to decrease in importance. However, soil pH proved to be the best predictor of habitat quality for plant species richness whereas the effect of other environmental variables often was rather low, and in many cases lower than that of the size of the dry grassland patch and/or isolation. For deciduous forests, DUPRÉ & EHRLÉN (2002) similarly found that soil pH was most closely correlated to species incidence within patches, whereas other soil parameters were rather unimportant. Several authors suggest that in Europe, the number of species adapted to base-rich substrates is distinctly higher than that adapted to acidic substrates (GRUBB 1977, GRIME 1979, TYLER 1996, EWALD 2003). We observed a strong effect of soil pH on species richness of vascular plants, bryophytes, and lichens. The relationship, however, was linear in cryptogams, but hump-back in vascular plants. In fact, a hump-back relationship between vascular plant species richness and soil pH is found by most other authors studying sufficient long pH gradients (TYLER 1996, DUPRÉ et

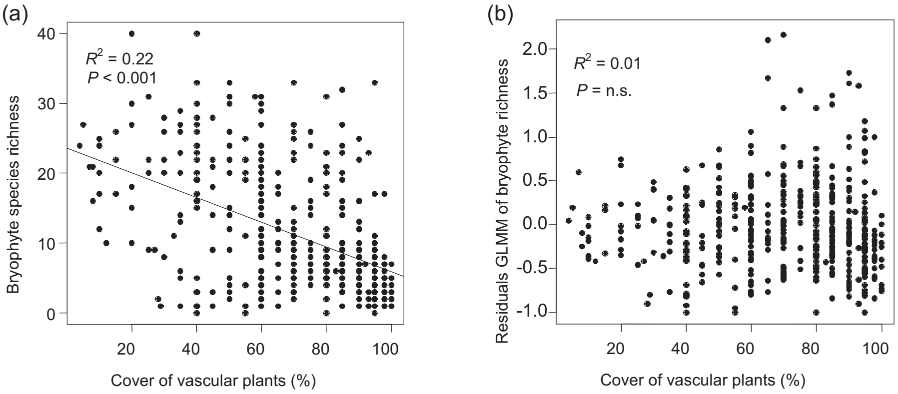


Fig. 4. Relationships of (a) bryophyte species richness and (b) residuals of the GLMM of bryophyte species richness with the cover of vascular plants.

al. 2002, Schuster & Diekmann 2003). In contrast, when studying small pH gradients, linear relationships are more likely (Gould & Walker 1999, Dupré et al. 2002). Furthermore, our results show that the response of vascular plant species richness to soil pH also depends on other environmental factors (Fig. 2): At high cover degrees of bare rock, vascular plant species richness showed a linear rather than unimodal response to soil pH. Bryophyte and lichen species richness increased with soil pH. In contrast, Gould & Walker (1999) record a negative effect of the soil pH on lichen species richness in different habitats in Canada. The optimum curve of lichen species richness and the cover of bare rock partly may be a sampling effect because we did not include epilithic crustose lichens in our study.

Positive effects of microtopography on vascular plant and bryophyte species richness support the hypothesis that spatial heterogeneity facilitates the coexistence of species through niche differentiation and thus enhances species richness (Grubb 1977, Tilman 1982, Tilman & Pacala 1993, Palmer 1994). Environmental conditions differed distinctly between “hummocks” and “hollows” with rather moist, loamy soils in “hollows”, and dry, sandy soils on “hummocks”. In a recent study, Lundholm & Larson (2003) similarly show positive relationships between within-plot heterogeneity and species richness in Canadian alvar grasslands. A pronounced microtopography, as mostly caused by frost action on poorly drained sites (Rosén 1982, Krahulec et al. 1986), probably also indicates those sites that are particularly wet in winter and thus do not only have a large spatial but also an extreme temporal heterogeneity in water supply. This may account for the co-existence of many species on small scales that otherwise would exclude each other (Dengler & Löbel 2006). Instability of sites with high microtopography may explain microtopography negative effect, on species richness of lichens, which often are very slowly growing.

It is surprising that we did not observe a significant effect of the type of management regime on species richness. Grazing and mowing are important forms of disturbance in grasslands, and disturbance is commonly considered a key factor for high local plant species richness (Connell 1975, Grubb 1977, Grace 1999). Many authors consider a moderate disturbance regime necessary for the preservation of dry grasslands (BOBBINK & WILLEMS 1988, WILLEMS 2001, POSCHLOD & WALLISDEVRIES 2002). A possible explanation may be the low number of mown compared with grazed plots included in our study (Table 1). Other studies show that vascular plant (DUPRÉ & DIEKMANN 2001) and bryophyte species richness (DURING & WILLEMS 1984, VAN TOOREN et al. 1990) of moderately grazed grasslands and wetlands is higher than those of mown sites. Another possible explanation could be that we – besides semi-dry grasslands as in most of the mentioned studies – also included a high number of *Sedo-Scleranthenea* stands. These are even less productive, and hence the management regime may have less distinctive effects on species richness. Instead, disturbance from frost and flooding may be the most important force in these kinds of habitats. In addition, in our classification of management regimes, we did not account for differences in grazing intensities, which also have been shown to be important (e.g. MCINTYRE & LAVOREL 1994 for grasslands, DUPRÉ & DIEKMANN 2001 for dry grasslands and coastal meadows).

Landscape structure and dispersal limitation

Neither the size of individual dry grassland patches nor the degree of isolation of sample plots could explain the significant spatial autocorrelation in vascular plant species richness. Possibly, the past landscape structure (about which we had no information), rather than the present distribution of dry grasslands, may have caused this spatial aggregation pattern. Different studies reveal a strong effect of site history on vascular plant species richness (PÄRTEL & ZOBEL 1999, BRUUN et al. 2001, COUSINS & ERIKSSON 2001). However, experimental data on the effect of dispersal limitation on vascular plant species richness of alvar grasslands are far from conclusive, with significant effects observed in some cases (ZOBEL et al. 2000), but not in others (PÄRTEL et al. 1998). ZOBEL et al. (2000) suggest that the effects of dispersal limitation depend on whether the local species pool is already impoverished or not. In southern Öland, dry grasslands are the most extensive in Scandinavia; in more fragmented landscapes, the effect of dispersal limitation on species richness of dry grasslands may be much more important (cf. KRAUSS et al. 2004). Furthermore, the relative importance of site availability and diaspore availability is scale dependent (MÜNZBERGOVÁ 2004), and effects of dispersal limitation may be first visible at larger scales, e.g. hundreds of square meters. Matrix effects may provide an additional explanation for the low effects of the size of individual dry grassland patches on vascular plant species richness (COOK et al. 2002). Adjacent vegetation types (mesophilous grasslands, fens, woodlands) are often quite rich in vascular plants but less rich in cryptogams. Thus, source-sink dynamics (PULLIAM 1988) may enhance small-scale vascular plant species richness at small dry grassland patches, and thereby counteract the impoverishment of small dry grassland patches in habitat specialists.

Although high dispersal abilities of cryptogams are generally assumed, our data suggest that this need not necessarily be the case. Similarly, several studies (SÖDERSTRÖM & JONSSON 1989, KIMMERER 1991, SUNDBERG 2005) show that a large proportion of bryophyte spores are deposited within a few meters from the source. Predominantly short distance dispersal is also reported for lichen soredia (ARMSTRONG 1987). From restoration projects of calcareous grasslands, different authors report that many typical bryophyte and lichen species do not invade the community (e.g. VAN TOOREN et al. 1990). In particular, pleurocarpous mosses, which often are asexually dispersed, seem to have rather low dispersal abilities and are often missing in diaspore banks (VAN TOOREN 1988, DURING 1997, 2001). Furthermore, gametophyte establishment rates from spores often are quite low (MILES & LONGTON 1990). Obviously, experimental studies on the effects of dispersal and establishment limitation in cryptogams confined to dry grasslands are needed.

Relationships between species richness patterns and vegetation cover

Relationships between species richness and vegetation cover suggest that interspecific competition is important both within and between taxonomic groups. However, negative relationships among taxonomic groups are often less obvious after correcting for the effects of environmental factors (Fig. 4). Thus, using raw species richness data may lead to an overestimation of the importance of interspecific competition in this type of study.

For all groups together as well as for vascular plants, bryophytes and lichens separately, we observed the typically assumed hump-back relationship (GRIME 1979, GRACE 1999) between vegetation cover and species richness of the taxonomic group in focus, at least in the residual analysis. This may indicate effects of interspecific competition. Alternative explanations are sampling effects due to a lower number of individuals per area, larger plant sizes on nutrient-rich sites (OKSANEN 1996, GOTELLI & COLWELL 2001) or smaller species pool sizes of nutrient-rich sites (TAYLOR et al. 1990). However, the hump-back relationship was even more pronounced after correction for environmental effects, and thus may indeed indicate effects of competition.

In vascular plants, the decrease in species richness with vegetation cover was only weak (Fig. 3). This could be because even the most productive sites of dry grasslands have so low biomass that competition does not play a major role in this type of habitat. Studying a longer nutrient gradient, e.g. by including mesophilous and eutrophic grasslands, probably would reveal a stronger hump-back relationship between vascular plant species richness and cover. Several studies suggest low competition among vascular plants in alvar grasslands (HUBER 1994, 1999). Our study supports this hypothesis. VAN DER MAAREL & SYKES (1993) explain this by the high tempo-spatial mobility of many short-lived alvar species allowing coexistence of a high number of ecologically equivalent species. WILSON et al. (2000) suggest that interspecific competition in semi-dry grasslands limits the biomass of each vascular plant species, but does not cause competitive exclusion.

A hump-back relationship between bryophyte richness and cover was also observed by INGERPUU et al. (2003), and RYDIN (1997) concluded in his review of competition studies among bryophytes that there is no indication that competition is less relevant in bryophytes than in vascular plants. Contrastingly, ØKLAND (1994) suggested positive interaction effects among bryophytes in coniferous forests. Similarly, analyzing permanent data from different habitats, e.g. earth banks and chalk grasslands, DURING & LLORET (2001) suggested that competitive exclusion rarely occurs in bryophyte communities. This apparent absence of competitive exclusion, however, may not be due to the lack of competition, but to a balance between competition and facilitation (DURING & LLORET 2001).

Our study suggests that competition between vascular plants and lichens is rather asymmetric. Dispersal limitation, low competitive ability, and an often very close association with certain habitat conditions, indicate that lichens are especially sensitive to the ongoing landscape alteration. Bryophytes seem to tolerate competition from vascular plants better than lichens. Furthermore, bryophytes may display a different phenological pattern than vascular plants, with increasing abundance of bryophytes with the moist, cool conditions of spring and autumn (AL-MUFTI et al. 1977). The positive effects of a dense ground layer on the establishment of vascular plants (VAN TOOREN 1988, RYSER 1993) may explain the positive relationship between vascular plant species richness and the cover of cryptogams. However, the effects of bryophyte cover are only weak and may depend on the dry grassland type. For example, OTSUS & ZOBEL (2002) record that a dense bryophyte layer has negative effects on the establishment of vascular plant seedlings in mesophytic basiphilous grasslands.

To conclude, plant species richness in dry grasslands is a complex phenomenon, influenced by numerous abiotic and biotic environmental factors. Our study shows that responses of species richness to single environmental factors depend both on the taxonomic group and on the combination of abiotic and biotic factors on a whole. Understanding the co-action of these factors is central while seeking for generalities in species richness patterns and to formulate guidelines for nature conservation applicable to a larger range of dry grassland types.

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