
Species-Richness Correlations of Six Different Taxa in Swedish Seminatural Grasslands

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Abstract: *An important question in conservation biology is whether the biodiversity of different taxa is correlated. We studied the extent to which the number of species of six different taxa—plants, birds, butterflies, bumblebees, ground beetles, and dung beetles—in 31 Swedish seminatural grasslands covary, and whether species diversity can be related to habitat variables. During 1996 and 1997, we surveyed plants and animals with appropriate techniques for each taxa and mapped the grassland habitat. In general, correlations between taxa were few. Grassland plant diversity (currently used as an indicator for conservation value) was only significantly positively correlated to total bird diversity. Bumblebee diversity was significantly positively related to both total and grassland butterflies, whereas there was a significant negative relationship between grassland birds and dung beetles. Plants, birds, bumblebees, and butterflies showed significant similarities in patterns of species composition, as did birds, butterflies, grassland butterflies, and ground beetles. The total number of plants and both subsets of birds (total and grassland) were significantly positively related to area, whereas there was a significant negative association between area and dung-beetle diversity. The diversity of both butterflies and bumblebees was significantly negatively related to the proportion of short-grazed field layer. Bumblebees showed a positive relationship with junipers, whereas ground beetles and grassland birds were negatively associated with trees. The total number of bird species was positively influenced by the occurrence of shrubs. Our results suggest that neither the species richness of grassland plants nor that of any other of the surveyed taxa can be used as an indicator for total biodiversity in seminatural grasslands. The lack of similar patterns of species composition among taxa also makes it difficult to define functional groups with similar habitat demands. Until we have more detailed knowledge of the demands of species and taxa, it is important that we direct management efforts so that we provide a wide spectrum of grassland characteristics.*

Correlaciones de Riqueza de Especies de Seis Diferentes Taxones en Pastizales Seminaturales en Suecia

Resumen: *Una pregunta importante para la biología de la conservación es si se correlaciona la biodiversidad de los distintos taxones. Estudiamos hasta donde varía y se relaciona el número de especies de seis diferentes taxones (plantas, aves, mariposas, abejas, escarabajos terrestres y coprófagos) con variables del hábitat en 31 pastizales seminaturales en Suecia. Durante 1996 y 1997 muestreamos plantas y animales mediante técnicas adecuadas para cada taxa y mapeamos el hábitat del pastizal. En general, las correlaciones entre taxones fueron pocas. La diversidad de plantas de pastizal (actualmente utilizada como un indicador de valor de conservación) sólo estuvo significativamente correlacionada positivamente con la diversidad total de aves. La diversidad de abejas se relacionó significativa y positivamente tanto con la diversidad total de mariposas y de pastizales, mientras que hubo una relación significativa negativa entre las aves de pastizal y los escarabajos coprófagos. Las plantas, aves, abejas y mariposas mostraron semejanzas significativas en cuanto a composición de especies, tales como las aves, mariposas, mariposas de pastizal y escarabajos terrestres. El total de plantas y ambos subconjuntos de aves (total y pastizal) se relacionaron significativa y positivamente con el área, mientras que hubo una asociación significativa negativa entre área y diversidad de*

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escarabajos coprófagos. La diversidad tanto de mariposas como de abejas se relacionó significativa y negativamente con la proporción del estrato de campo poco pastoreada. Las abejas mostraron una relación positiva con árboles, mientras que los escarabajos terrestres y las aves de pastizal se asociaron negativamente con los árboles. El total de especies de aves estuvo influenciado positivamente por la ocurrencia de arbustos. Nuestros resultados sugieren que ni la riqueza de especies de plantas de pastizal ni los otros taxones muestreados pueden ser utilizados como un indicador de la biodiversidad total de pastizales seminaturales. La falta de patrones similares en la composición de especies entre taxones también dificulta la definición de grupos funcionales con demandas similares de hábitat. Mientras no haya conocimientos más detallados sobre las demandas de especies y taxones, es importante que dirijamos nuestros esfuerzos de manejo a proporcionar un amplio espectro de características de los pastizales.

Introduction

An important question in conservation biology is whether certain well-known and easily surveyed taxa can be used to predict overall biodiversity (Noss 1990; Tracy & Brussard 1994; Faith & Walker 1996; Pharo et al. 1999). Because there is never enough funding, time, or taxonomic knowledge to study the biodiversity of all taxa, conservation biologists have tried to find a limited set of organisms that can be used as indicators for overall biodiversity (Kremen 1992; Pearson & Cassola 1992; Prendergast et al. 1993; Faith & Walker 1996). Several taxa—such as plants, birds, tiger-beetles, and butterflies—have been suggested as such indicator taxa (Kremen 1992; Pearson & Cassola 1992; Blair 1999; Pharo et al. 1999).

Is there support in the literature for covariation of species richness among taxa? The species-area effect (Williams 1943)—the positive relationship between area sampled and species richness—could lead to covariation in species numbers. In addition, habitat heterogeneity may have a positive effect on species richness (Williams 1964); if this is important for several taxa, it could lead to covariation within taxa when sites of varying heterogeneity are compared. Although the exact ratio between the number of predator and prey species in a community has been a matter of discussion (Pimm 1991), a more species-rich prey assemblage should support more species-rich predator assemblage, which could also lead to covariation in species numbers among taxa. One could also argue that no relationship among taxa is to be expected. Different taxa and species are known to be limited by different habitat requirements (e.g., certain resources) or processes (e.g., fire regimes or grazing) (Hengeveld 1996; Lambeck 1997), making it less likely for the species richness of different taxa to covary. Also, differences in scale dependence (e.g., differences in species area requirements; Wiens 1989) can result in different patterns of diversity among taxa. Finally, habitat fragmentation may influence species numbers differently. Launer and Murphy (1994) suggest, in a study of natural grasslands, that there are few reasons to assume that

plant and animal species in habitat remnants should respond to fragmentation in the same way. Thus, ecological theory is both in favor of and against the expectation of covariation among different taxa.

The concept of indicator taxa assumes that high diversity in one taxon is associated with high diversity in other taxa (Noss 1990; Pearson & Cassola 1992), but the literature on the association between species diversity among taxa is inconclusive. In observational studies, both positive relationships between taxa (Pearson & Cassola 1992; Väisänen & Heliövaara 1994; Nilsson et al. 1995; Berg & Tjernberg 1996; Duelli & Obrist 1998; Robbins & Opler 1997; Blair 1999; Pharo et al. 1999) and a lack of relationship (Usher 1992; Prendergast et al. 1993; Saetersdal et al. 1993; Prendergast & Eversham 1997; Robbins & Opler 1997; Howard et al. 1998; Lawton et al. 1998; Niemela & Baur 1998; Tardif & DesGranges 1998; Jonsen & Jonsell 1999) have been reported. Possible reasons for these varied results include differences in the type of diversity estimate used, the selection of taxa, and the temporal and spatial scales at which the studies were performed (Flather et al. 1997).

Seminatural grasslands are the subject of great conservation concern in Europe. The intensification and expansion of agriculture in Europe over the last 40 years has greatly modified agricultural landscapes. The area of seminatural grassland has decreased dramatically, and this loss is a threat to the large number of species dependent on this habitat. In Sweden the area of managed seminatural grasslands had until 1989 decreased to less than half of the area recorded in the 1920s, and 20% of the remaining grassland was not managed (Statistics Sweden 1989), implying a radical change in the landscape. When a seminatural grassland is abandoned, a succession starts that ultimately leads to forest. Seminatural grasslands used to be important sources of livestock fodder, and many have been managed continuously for centuries. Swedish seminatural grasslands are heterogeneous both in the field layer and with respect to shrubs and trees. The plants and animals that live in seminatural grasslands originate from a wide range of natural habitats (e.g., Ekstam et al. 1988). Several hundred species of

plants, fungi, and animals in seminatural grasslands are found on the Red Data Lists in Sweden (Ehnström et al. 1993; Ingelög et al. 1993; Aronsson et al. 1995). Many of these species have today lost their original habitat and are therefore restricted to seminatural grassland.

Until now, the conservation priorities and management demands of Swedish seminatural grasslands have been based mainly on floral considerations and traditional management (Ekstam & Forshed 1996), although the goal is to preserve overall biodiversity. Because seminatural grasslands are anthropogenic habitats, long and continuous management has been expected to result in an overall high biodiversity of pasture organisms. Relationships between the flora and other taxa are poorly known, however. We know of two studies that took into account several taxa in Swedish seminatural grasslands. Pärt and Söderström (1999a) showed that there is no association between nature-conservation values based on floral qualities and bird species richness, and the regional council of Kalmar (Länstyrelsen i Kalmar län 1996) reported that many seminatural grasslands with high butterfly and fungal diversity are not covered by a national inventory based on floral values.

We investigated whether the species richness of six different taxa found within 31 seminatural grasslands in south-central Sweden covaries. Our main objective was to test the suitability of grassland plants as indicator taxa for overall biodiversity. Apart from plants, we chose five taxa that represent an important part of the biodiversity in seminatural grasslands: birds, butterflies, bumblebees, dung beetles, and ground beetles. We analyzed a subset of species characteristic of grasslands and the total number of species when it was feasible. Furthermore, we examined whether the species richness of different taxa was associated with grassland characteristics that are important from a conservation point of view: area, field-layer heterogeneity, and habitat characteristics affected by management, such as grass height and area covered by shrubs and trees.

Methods

Study sites

We performed our study in 31 grazed seminatural grasslands in an agricultural farmland landscape within 40 km of Uppsala (lat. 59°52'N, long. 17°39'E) in south-central Sweden. These seminatural grasslands (hereafter referred to as pastures) were surveyed during 2 consecutive years, 1996–1997, and in 8 of the pastures during both years. We tried to select pastures to cover the variation in habitat characteristics and management regimes of pastures in this region, but selected pastures did not differ from a larger selection of pastures in the region in habitat area or vegetation structure (i.e., grass height,

shrub, and tree cover) (*t* tests, *df* = 113, *p* > 0.30, in all cases).

Surveys

VASCULAR PLANTS

In 1997 we surveyed pastures systematically for all vascular plant species. The survey time was roughly proportional to the area of the seminatural grassland. Swedish pastures are heterogeneous, and efforts were made to visit all types of field-layer vegetation within the grasslands. To find the smallest heavily grazed plants in the sward, we placed 1 × 1 m plots in the most common plant communities (>0.5 ha). We carefully searched these plots for all species. The number of plots were in proportion to the area of the vegetation type within the pasture (2 plots/ha). Grassland plant species were defined according to the set of plants used as indicators of valuable seminatural grasslands in Uppsala county (e.g., Länstyrelsen & Uppsala län 1993). This subset comprised about one-tenth of the total number of species.

BUMBLEBEES AND BUTTERFLIES

Bumblebees (*Bombus* and *Psithyrus*) were sampled in July 1996 and 1997 and butterflies (*Hesperiidae*, *Pieridae*, *Nymphalidae*, *Satyridae*, and *Lycaenidae*) in July 1997 (*n* = 20 pastures). This period represents peak flight activity of bumblebees and butterflies in south-central Sweden. Sampling was performed by the transect method (Banaszak 1980). The surveyors walked along a square route (100 × 100 m), subjectively located in a part of each pasture representative in terms of the composition and diversity of grass height, amount of tree and shrub cover, and vegetation types. Walking speed was 20 m per minute, and all bumblebees and butterflies within 1 m of the transect were counted. The surveys were conducted between 0900 and 1900 hours, only during fair weather (i.e., light winds, no precipitation, temperatures 14–27° C). Pasture routes were visited 13 times in 1996 and 18 times in 1997. All pastures were visited on the same day, and time of the day varied according to a randomized schedule. The number of species reached an asymptote between 5 and 10 visits, so we did not compensate for the number of visits.

The nomenclature for bumblebees follows that of Løken (1973). The bumblebee species *Bombus lucorum* and *B. terrestris* were grouped together because they are difficult to identify in the field. No grassland subset was selected for bumblebees because of the low total species number. Three species pairs of butterflies could not be distinguished in the field (*Fabriciana adippe* and *Mesoacidalia aglaja*, *Clossiana selene* and *C. euphrosyne*, *Plebejus argus* and *P. idas*). These species were therefore regarded as three morphospecies (Oliver & Beattie 1996) in the analyses. For butterflies, nomen-

clature follows that of Gustavsson (1994). A grassland subset of butterfly species was selected according to the method of Dal (1978).

DUNG BEETLES

Dung beetles were sampled in June 1996 and 1997. We surveyed only pastures where there were grazing cattle (i.e., fresh dung) at the time of sampling ($n = 28$ pastures). The early summer dung-beetle assemblage was chosen because it is the most species-rich in north-temperate climates. Ten randomly chosen dung pats approximately 3 days old were collected from each pasture. To minimize the influence of weather and seasonal effects on the fauna, four randomly chosen pastures were sampled per day during a limited time period. We extracted all beetles from the pats by floating the pats in water and collecting the beetles that floated to the top and all beetles from beneath the pats by digging for specimens in the soil (Wiktelius 1998). Only dung beetles of the families Scarabaeidae and Geotrupidae were used in statistical analyses. The Scarabaeidae are dung specialists that, compared with other dung-living insects, have a relatively well-known ecology and conservation status (Hanski & Cambefort 1991). No grassland subset was selected for dung beetles because of the low total species number.

GROUND BEETLES

Ground beetles, Carabidae, were collected in 1997 in 20 randomly located pitfall traps in each pasture. Traps consisted of plastic cups (8 cm in diameter and 9.5 cm deep) filled with water, detergent, and coarse-grained salt (a preservative). Pitfall traps were set for 2 weeks in early June and August, respectively. During both periods the traps were emptied after 1 week and after 2 weeks. Ground beetles from each trap were pooled over all sampling events. Livestock trampled a large number of traps in seven pastures, so these pastures were excluded from further analyses. Among the remaining pastures, damage was distributed evenly over sampling events and traps. Although the number of ground-beetle species was not significantly related to the number of undamaged traps in this subset (regression, adjusted for degrees of freedom: $R^2 = 0.03$, $p = 0.22$), we accounted for the effect of number of traps on species richness by using residual species richness as the dependent variable. The subset of specialist ground beetles in seminatural grasslands was selected based on expert advice.

BIRDS

We surveyed each pasture for birds on seven occasions between 20 April and 1 July in both 1996 and 1997. We used territory mapping where song and other indications of breeding are used to establish the number and position of territories (Svensson 1975; Bibby et al.

1992). All counts were performed between sunrise and 1000 hours, and the time spent surveying in each pasture was about 10 minutes per ha and count (for details see Pärt & Söderström 1999b). All pastures were visited in the same day, and the time of the day varied according to a randomized schedule. We recorded the number of territories of 29 grassland bird species for which grasslands were judged important as breeding or foraging habitat (cf. Robertson & Berg 1992; Pärt & Söderström 1999a). For the remaining 35 species (mostly forest species), we noted presence or absence.

Habitat Mapping

The pasture area covered by trees and shrubs, respectively, was recorded on maps (1:2500) during field visits and with the help of aerial photographs (1:30,000). Shrubs were classified as junipers (*Juniperus communis*) or thorny shrubs, mainly sloe (*Prunus spinosa*) and roses (*Rosa* spp.). Tree and shrub variables were expressed as proportions of the pasture area (Table 1). Grass height—reflecting grazing pressure—was estimated visually during the last week of June as the proportion of the open area where the height of the grass was <5 cm. This was done in a grid of 1-ha quadrates covering the entire pasture (Table 1; for details see Pärt & Söderström 1999b). To estimate field-layer heterogeneity, we counted the number of vegetation communities were counted according to classification of the Nordic Council of Ministers (Nordiska Ministerrådet 1998) (Table 1).

Statistical Analyses

Species numbers did not differ between years in pastures surveyed both years (Wilcoxon test, $n = 8$, $p > 0.18$ in all tests), so data from both years were pooled. Survey data from 1997 were used in cases where pastures were sampled both years (the alternative of using mean values for 1996 and 1997 did not change the main results).

Table 1. Descriptive statistics of area and habitat variables of 31 seminatural pastures in south-central Sweden.

Variable	Mean	SE	Minimum	Maximum
Area (ha)	5.58	0.12	0.50	12.72
Field layer				
heterogeneity	5.48	0.23	3	8
(number of vegetation types)				
Grass height ^a	0.48	0.046	0	0.95
Junipers ^b	0.013	0.0022	<0.001	0.043
Thorny shrubs ^b	0.0092	0.0027	0	0.064
Trees ^b	0.20	0.028	0	0.54

^aProportion of the open grassland area where grass height is <5 cm in the last week of June.

^bProportion of area of the pasture covered.

We tested spatial independence by comparing a similarity matrix based on Sørensen's similarity index (presence or absence of species) with a matrix containing the pair-wise distances between pastures measured from a map. The comparison was made with the Mantel test (PC-ORD for Windows 3.19; McCune & Mefford 1997). This method was also used to investigate patterns of species composition among taxa, and then pair-wise comparisons were made between similarity matrixes for each taxa. We used Pearson correlations to test whether the species richness of different taxa covaried.

Associations between the number of species of different taxa and pasture area and habitat variables were analyzed by multiple linear regression. There were no significant correlations among independent variables (all $r < 0.30$, $p > 0.10$), except for a significant positive relationship between area and proportion of thorny shrubs ($r = 0.39$, $p = 0.03$). Independent variables were grouped into three sets of logically interrelated variables: (1) pasture area, (2) field-layer variables (i.e., grass height and number of vegetation types), and (3) vegetation-structure variables (i.e., proportion of pasture covered by trees, thorny shrubs, and junipers, respectively). To meet the assumptions required for parametric tests, pasture area was $\log_{10}(x+1)$ -transformed, proportional variables were arcsine-transformed, and the species numbers of all taxa were $\log_{10}(x+1)$ -transformed prior to regression analysis. For each taxa, we constructed six regression models in which the above sets of variables were tested in different order. Variable selection within each set was done through a stepwise procedure, and significance to enter and remove variables was set at 0.10 and 0.15, respectively. The results were highly robust in that, for all taxa, the same predictor variables were selected regardless of the order of testing. We also tested whether species richness was quadratically associated with habitat variables, but the quadratic term did not significantly associate with species number ($p > 0.10$) for any taxa. All residuals were checked for deviations from normality and homoscedasticity. We con-

trolled for area effects by using residuals from regression with area. Statistical analyses were done with SPSS version 6.1 (Norusis 1994).

We made many tests on the same data set, thereby increasing the risk of significant results occurring by chance (Zar 1984). We believe, however, that decreasing the significance level would have resulted in an even higher risk of ignoring real relationships.

Results

We found 579 species in 31 seminatural grasslands: 386 vascular plants, 14 dung beetles, 74 ground beetles, 30 butterflies, 11 bumblebees, and 64 birds (Table 2). There was no significant relationship between the spatial distribution and species composition of grasslands (Mantel test, Table 4). Within taxa, there were significant positive correlations between the richness of grassland species and remaining species for plants and butterflies but not for birds and ground beetles (Table 3).

Significant relationships between the species richness of taxa were few (Table 3). The diversity of grassland plants was significantly related only to total number of bird species (Table 3). Furthermore, the total number of plants and total number of bird species showed a significant positive correlation, as did those of bumblebees and both subsets of butterflies. Dung beetles and grassland birds, however, were significantly negatively associated. Plants and birds were surveyed with a constant effort per hectare, whereas all insect taxa were surveyed with a constant effort per pasture, regardless of its area (see methods). This might confound intertaxa correlations, but controlling for area effects of different taxa by using the residuals of the regression of species richness on pasture area did not change the main results (i.e., significant results did not become nonsignificant, or vice versa). The only exception was the significant positive correlation that arose between species richness of all butterflies and all plants when area was accounted for ($r = 0.50$, $p = 0.03$).

Table 2. Number of observed species in seminatural grasslands (pastures) studied in south-central Sweden.

<i>Taxa</i>	<i>Mean</i>	<i>SE</i>	<i>Minimum</i>	<i>Maximum</i>	<i>n (pastures)</i>
All species					
plants	129.71	3.99	94	180	31
ground beetles	15.63	0.81	8	22	24
dung beetles	8.14	0.29	5	11	28
butterflies	18.00	1.10	6	24	20
bumblebees	5.77	0.30	2	9	31
birds	20.87	0.89	12	32	31
Grassland species					
plants	16.32	0.80	8	25	31
ground beetles	5.25	0.39	2	9	24
butterflies	11.95	0.81	4	16	20
birds	10.65	0.61	5	17	31

Table 3. Correlation matrix for species richness of plants, insects, and birds in 31 seminatural grasslands^a in south-central Sweden.^b

Variable		Plants		Ground beetles		Dung beetles	Butterflies		Bumblebees	Birds
		A	G	A	G	A	A	G	A	A
Plants	G	0.54**								
Ground beetles	A	-0.08	-0.12							
	G	-0.09	-0.25	0.13						
Dung beetles	A	0.10	0.12	0.10	0.13					
Butterflies	A	0.36	0.32	0.08	-0.2	0.45				
	G	0.32	0.27	0.08	0.02	0.40	0.74***			
Bumblebees	A	0.20	0.10	-0.07	-0.28	0.17	0.52*	0.49*		
Birds	A	0.53**	0.42*	-0.06	-0.22	-0.18	0.24	0.13	0.13	
	G	-0.06	-0.13	-0.10	-0.05	-0.50**	-0.29	-0.23	-0.22	-0.28

^aExcept for ground beetles, dung beetles, and butterflies, which were sampled in 24, 28, and 20 seminatural pastures, respectively (see Table 1).

^bWhen the two subsets of respective taxa are compared, the grassland subset is withdrawn from total number of species. Probability: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. Abbreviations: A, all species found; G, only grassland species found.

The taxa that showed significant positive correlations of species richness—plants and birds, butterflies and bumblebees, respectively—also showed significant similarities in the patterns of species composition analyzed with a Mantel test (Table 4). In addition, all birds showed corresponding patterns of species composition with both subsets of butterflies, as did ground beetles with grassland butterflies (Table 4).

Multiple-regression models showed that the total number of plant species and total number of grassland bird species, respectively, were significantly associated with increased pasture area (Table 5). The number of dung-beetle species, in contrast, decreased with increasing pasture area (Table 5). Field-layer heterogeneity was negatively associated with the species richness of grassland birds and positively associated with total number of plants. In pastures with a higher proportion of the field layer consisting of short vegetation (<5 cm), there were fewer species of butterflies and bumblebees (Table 5). Total bird species richness was positively influenced by the proportion of the area covered by junipers and thorny shrubs, whereas there were fewer species of grassland birds and grassland ground beetles in pastures with a higher proportion of tree cover. Bumblebees were positively associated with a high proportion of junipers (Table 5).

Finally, to investigate whether the negative correlation between dung beetles and grassland birds (Table 3) might be due to avian predation on dung beetles, we extracted a subset of ground-foraging, insectivorous bird species: Fieldfare (*Turdus pilaris*), Blackbird (*Turdus merula*), Starling (*Sturnus vulgaris*), Jackdaw (*Corvus monedula*), Hooded Crow (*Corvus corone cornix*), and Magpie (*Pica pica*). The number of species of this subset, however, was not significantly associated with the number of dung-beetle species ($r = -0.22$, $n = 25$, $p = 0.30$), and the total abundance of these birds was not related to the abundance of dung beetles ($r = 0.20$, $n = 25$, $p = 0.34$).

Discussion

Our study suggests that it is difficult to find appropriate indicator taxa for evaluation of total biodiversity on a local scale in Swedish seminatural grasslands. Our results show a low degree of covariation in species numbers among taxa, a pattern consistent among the grassland subsets of species. Invertebrates do not show any significant relationship with grassland plants, and although total number of birds and grassland plants do covary, a considerable part of the variation is still unexplained ($r = 0.41$). Differences in sampling effort in relation to area between birds and plants and the insect taxa could have made associations between numbers of bird and plant species and those of the insect taxa less apparent. Area compensation of the data did not change the main results, however. Therefore, we believe that it is not likely that differences in sampling effort had a great effect on our results. Also, the species composition of taxa was related in only a few cases. This indicates that different factors influence the occurrence of species in the studied taxa. Hence, using grassland plants as indicator taxa in Swedish seminatural grasslands will not give satisfactory estimates of total biodiversity.

The species richness of the studied taxa showed different relationships with grassland characteristics (area, field-layer heterogeneity, and different habitat factors; grass height; cover of trees and shrubs). Significant positive species-area relationships occurred in the total number of bird species and grassland birds and in the total number of plants. Because area and field-layer heterogeneity were not significantly correlated, the species richness-area effect was an effect of a larger area containing a larger number of individuals, rather than an effect of increased field-layer heterogeneity with increased area. The significant negative relationship between the number of dung-beetle species and area has not been shown before and has no obvious explanation; perhaps the

Table 4. Analysis of similarity patterns (Mantel test t)^a in species composition^b among taxa and spatial independence within taxa in 31 seminatural grasslands in south-central Sweden.

	Plants		Ground Beetles		Dung beetles	Butterflies		Bumblebees	Birds		
	A	G	A	G	A	A	G	A	A	G	
Species composition patterns ^c											
plants	G	+6.58***									
ground beetles	A	+1.00	+0.84								
	G	+0.63	-0.17	+5.55***							
dung beetles	A	-0.78	+0.03	-1.88	-1.48						
butterflies	A	+1.75	+1.77	+1.93	+0.36	+0.30					
	G	+1.58	+1.87	+2.28*	+0.43	+0.14	+5.21***				
bumblebees	A	-0.11	-0.05	+0.73	-0.59	+1.93	+2.19*	+1.95			
birds	A	+5.01***	+4.14***	+1.51	+1.61	-1.02	+3.05**	+2.68**	+0.68		
	G	+1.14	+0.88	+1.15	+1.74	-0.83	+0.99	+0.66	+0.13	+7.08	
Spatial independence ^d											
distance		+0.60	+0.94	+0.39	-0.81	-0.12	-0.52	-0.29	+0.33	-0.72	-0.37

^aSigns indicate positive or negative similarities in species-composition patterns; a value close to zero indicates indifference. For each comparison, the grassland with missing data for one or both of the variables was excluded. Numbers of rows and columns therefore vary between 15 and 31. Probability: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

^bAbbreviations: A, all species found; G, only grassland species found.

^cSimilarity matrixes were constructed for each taxa with Sørensen's similarity index (presence/absence). The similarity matrixes were compared pair-wise by Mantel test.

^dAnalysis of spatial distribution of grasslands (linear distance) and species-composition patterns (calculated with Sørensen's similarity index [presence/absence]) was performed by Mantel test.

large and small pastures in our sample differ in some unknown factor important to dung beetles.

Because vegetation types are defined by plant communities, the positive relationship between total number of plant species and field-layer heterogeneity was expected. The invertebrate taxa were not related to field-layer heterogeneity, whereas grassland birds were negatively re-

lated to heterogeneity. We believe that habitat heterogeneity is important to species richness of all taxa, but that different taxa are related to different kinds of heterogeneity (e.g., diversity of birds is related to structural heterogeneity; MacArthur 1958; Rosenzweig 1995).

Both butterflies and bumblebees were negatively influenced by the proportion of short grass. Heavy grazing

Table 5. Multiple-regression analyses of relationships^a between species number and pasture area and heterogeneity and management habitat variables in 31 seminatural grasslands^b in south-central Sweden.

Taxa ^c	R ² (%)	Area	Field layer		Shrubs		Trees
			heterogeneity	grass height	junipers	rose/sloe	
Plants							
A	27.1**	0.36*	0.35*				
G	—						
Dung beetles							
A	23.7*	-0.49*					
Butterflies							
A	32.9**			-0.57**			
G	28.4**			-0.53*			
Bumblebees							
A	23.8*			-0.36*	0.37*		
Ground beetles							
A	—						
G	21.4*						-0.46*
Birds							
A	50.1***	0.35*			0.31*	0.52**	
G	44.8***	0.47**	-0.45**				-0.38*

^aVariance explained by the model (R²) and standardized partial-regression estimates are shown for variables with $p < 0.05$. Probability: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

^bExcept for ground beetles, dung beetles, and butterflies which were sampled in 24, 28, and 20 seminatural pastures, respectively (see Table 2).

^cAbbreviations: A, all species found; G, only grassland species found.

reduces the frequency of flowering in field-layer plants, thereby decreasing important supplies of nectar and pollen. The amount of nectar influences the abundance of butterflies (Holl 1995) and bumblebees (Teräs 1985), and the diversity of flowering plants influences the diversity of butterflies (Kremen 1992).

The occurrence of shrubs was important for the number of bird species, which is in accordance with several earlier studies (e.g., O'Connor & Shrubbs 1986; Pärt & Söderström 1999b). The number of grassland birds (compare with Pärt and Söderström 1999a, 1999b) and grassland ground beetles decreased with the increased proportion of the pastures covered by trees, whereas the species numbers of bumblebees were positively related to the proportion of junipers. Hence, the tree and shrub layer was important to the diversity of several taxa, but the patterns differed among taxa.

In the introduction we presented a few factors that may result in, or counteract, covariation of diversity among taxa. One was that many species in one trophic level may result in many species in the higher trophic level, thus leading to covariations in species numbers among taxa. In our study the positive relationship between the number of plant and butterfly species after area compensation could be considered such an example (the literature on this relationship is inconclusive however; Thomas and Mallorie [1985] vs. Sharp et al. [1974] and Kremen 1992). The opposite process, in which predation decreases the number of prey species, did not seem the obvious cause of the negative correlation between grassland birds and dung beetles. The most evident reason for covariation of species richness between taxa in our study, however, did seem to be mutual habitat dependencies. Plants and birds both showed a positive area relationship, and butterflies and bumblebees showed a common negative relationship with grass height. Also, the species compositions of these taxa were related (Table 4), which indicates that not only species numbers are correlated among the taxa but that grasslands with certain qualities harbor specific species pools from both taxa. This was evident when we analyzed habitat preferences of single species. For example, the occurrence of several butterfly species (e.g., *Lycaena hippothoe*, *Lasiommata maera*, *Issoria lathonia*) and bumblebee species (*Bombus pratorum*, *Bombus lapidarius*) was negatively associated with grass height in seminatural pastures (A.G., unpublished results).

Management and Conservation Implications

Until now, habitat requirements of the flora have dominated the management directives given for Swedish seminatural grasslands. Our results suggest that it is important that we not impose a single management strategy on all seminatural grasslands. Instead, we should continue

to manage seminatural grasslands so that they represent a wide spectrum of seminatural grassland types with differences in tree and bush cover and variation of grazing pressure in space and time. It is also important to note that small seminatural grasslands can be as important per unit area as large ones to insect species diversity. Although bumblebee and butterfly diversity was negatively influenced by intensive grazing, ceasing management efforts is not an option. Regular disturbance through management efforts is crucial to maintaining the species diversity of butterflies, and abandonment of seminatural grasslands has led to the disappearance of grassland specialist butterflies (Erhardt 1985; Swengel 1998). The reason for the disappearance of butterflies might be that important larval food plants need sward management to sustain their populations (Schwarzwälder et al. 1997).

Our results suggest that it may be difficult to find an indicator taxon that can be used to predict overall biodiversity in seminatural grasslands. The lack of correlation in species composition among taxa also makes it difficult to select functional groups of species (associated with common habitat factors) at this point. We do believe, however, that it is important to make a deeper evaluation of the relationships among species, taxa, and different habitat factors to try to find crucial factors connected with the occurrence of certain species and diversity of taxa.

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