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Patterns of species richness in dry grassland patches in an agricultural landscape

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Eighty-five patches of semi-natural grassland of varying size scattered in a agricultural landscape were investigated for their flora of vascular plants. Relationships between species richness and patch area, spatial isolation and local habitat conditions including heterogeneity were examined. Differences between single species and among groups of species defined by life-history traits were also investigated.

Area was shown to be an important determinant of species richness irrespective of habitat heterogeneity. Isolation in space and habitat heterogeneity also play significant roles. These results are consistent with results from a multitude of studies on fragments of ancient deciduous woodland in northern Europe. They are, however, contradictory to results from previous studies in grasslands within the same region.

Seed mass and dispersal syndrome were poor predictors of the degree to which the species were affected by isolation of grassland patches. Seed mass deviation from community median could explain a small percentage of the variation in regional abundance. Logistic regression on species occurrences showed that few species are associated with large patches, and less than half seem to avoid isolated patches.

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The positive relationship between island area and species richness has been well-established for a long time. There has for almost as long a time been much controversy over the explanation for it. MacArthur and Wilson (1963, 1967) proposed their theory of island species richness as an equilibrium between immigrations and extinctions. A contrasting explanation for the positive species-area relationship is a positive relationship between species number and number of habitats and between number of habitats and island area (Williams 1943). Kohn and Walsh (1994) found habitat diversity to be of minor importance compared to log area on true islands. Köchy and Rydin (1997) found that habitat diversity was more important than an immigration-extinction equilibrium in Swedish grassland "islands" in an agricultural landscape.

Recently views have broadened, and a theory of metacommunities (Holt 1997) built up of metapopulations (Hanski 1999) is emerging. This puts emphasis on differences among species, which may have different regional population dynamics depending on population longevity and dispersal ability in space and time (Eriksson 1996). Many plant species associated with temperate grasslands exhibit strong clonal growth making the potential life-span of genets and hence population almost infinite. In a recently fragmented habitat long-lived species may be less negatively affected by the diminished habitat area as short-lived species. Many species have persistent seed banks, enabling them to overcome extended unfavourable periods. In the same way such species could be hypothesised to be less affected by shrinking habitat area than species with transient seed banks. Isolation of fragments is likely to act differentially upon species with different dispersal abilities. Dispersal ability is difficult to assess. Traditionally focus has been on the dispersability of single propagules and on dispersal vectors, such as wind or animals. Colonisation success of plant species must,

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however, be determined by seed production (inversely related to seed mass due to a trade-off) and recruitment rate (positively related). From these observations Eriksson and Jakobsson (1998) hypothesised that species with intermediate seed mass (and seed production) gain the highest regional abundance. They found support for this in a study of central Swedish grasslands.

The present paper addresses four interrelated questions: 1) what proportions of the variation in species richness are explained by area and isolation vs site conditions including habitat heterogeneity? 2) Is the relative importance of area, isolation and site conditions the same for groups of species with different traits associated with persistence or dispersability? 3) Is the relative importance of area, isolation and site conditions the same for all grassland species? 4) Can the regional abundance of species be explained by deviation in seed mass from the community median seed mass?

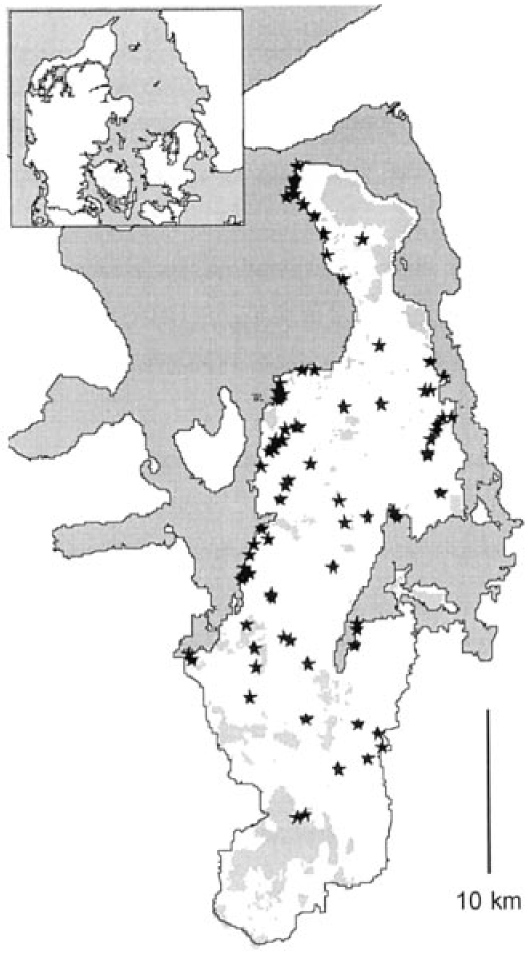

Fig. 1. The study area. Stars denote patches of semi-natural grassland on well-drained soil and the grey shade shows forest cover.

Material and methods

Study area

The studied area (Fig. 1) is ca 10 × 40 km situated on the island Sjælland in eastern Denmark (12°E, 55°45′N) as a peninsula between two inlets (ca 5‰ salinity). The climate is temperate. Mean annual temperature and precipitation is ca 8.0°C and 575 mm respectively. There is a net annual precipitation surplus, except for in south-facing sandy slopes. Land-uplift has been 0.5–1 m since the Weichselian glaciation.

Patches of semi-natural grassland occur scattered throughout the study region. They mostly occur on areas barely accessible to agriculture due to topography. That is often on steep slopes, mainly fixed coastal slopes from the Littorina transgression. Other important occurrences are on Bronze-age burial mounds, which are circular vaulted mounds 5–15 m in diameter and 2–5 m high, originally built of sods. The burial mounds have in most cases been unmanaged for decades. All other sites are grazed by livestock or have been so until recently. In all cases soils are deep till soils, varying from sandy to clayey and varying in calcite content from zero to ca 20%. The traditional management is livestock grazing.

Data collection

All sites of dry semi-natural grassland (a total of 169 sites, mainly pointed out by county surveys of protected habitats) were visited in the summer 1996. Of these 85 were chosen according to two criteria: no traces of ploughing or fertilisation, and, if ungrazed, only moderate successional changes in vegetation structure. Burial mounds with scrub cover above two thirds of their area were discarded.

A significant proportion of grassland sites present in the Danish landscape are former arable fields (Ejrnæs and Bruun 1995), and strong differences in vegetation composition corresponding to site age are expectable (Gibson and Brown 1991, Ejrnæs and Bruun 1995). To avoid confounding effects of recent management history on differences in species richness due to processes on a larger temporal scale, all young sites were excluded by inspection of 1945 aerial photographs. The area percentage under agriculture was at its maximum in Denmark in the 1930s and 1940s. Areas not cultivated during that period are unlikely to have been so both earlier and later.

In the field, a species list was made from each selected site on two to four visits during 1996–97. The time spent at each site was adjusted to be proportional to its size and topographical heterogeneity. Species confined to nutrient-enriched spots were not recorded. At each site between two and ten soil samples were taken while attempting to cover the ranges in soil acidity and texture of the site. Soil pH was measured electrometrically in a 1:2 water suspension (fresh soil: demineralised water). Only the site's maximum and minimum pH values were used. From the same samples the soil texture was scored subjectively in five classes (in order of increasing score: coarse sand, sand, clayey sand, sandy clay, and clay). Angle of slope and aspect (both in degrees) were measured at a number of places, again attempting to cover the within-site variation from steep south-facing to steep north-facing slopes. The angle and aspect of slope were used to compute the potential direct solar radiation at equinox in the same way as done by Ejrnæs and Bruun (2000). This is an easy-to-measure and fairly good approximation of water status and drought proneness of a site. Only the site's maximum and minimum values of potential radiation were used in the analyses. Soil pH and potential solar radiation has been shown to be by far the two most important variables accounting for species composition at the community scale in old unimproved Danish grasslands (Ejrnæs and Bruun 2000). As site descriptors were used: mean (of max. and min. values) soil pH and potential radiation, median soil texture and the maximum inclination of slope. Two additional site descriptors were calibrated from the species lists using the indicator values from Ellenberg et al. (1992): temperature ($Temp^{cal}$), and soil nitrogen (N^{cal}). The calibrated value was the unweighted mean of values for species present at the site and having a value in Ellenberg et al. (1992) different from "x" (indifferent species).

The within-patch habitat heterogeneity was computed in the following way. The overall observed pH range from 4.5 to above 8 was divided in two, "neutral" (max. $pH < 7.0$) and "calcareous" (min. $pH > 6.8$), in accordance with the point of major change in plant availability of soil P and Fe (Tyler 1996). The potential radiation was divided in classes of low, intermediate and high. Using maximum and minimum site values for soil pH and potential radiation, the number of pH and radiation classes of a site was counted and these two figures multiplied. A site with both neutral and calcareous soil, and both south-facing and north-facing slopes (hence also level areas), would thus get the score six for habitat heterogeneity. This variable was log transformed to ensure a better fit to the normal distribution. The number of soil texture classes observed at the sites was counted and used as an additional estimate of habitat heterogeneity.

A number of area and isolation characteristics were computed from the geographical co-ordinates and the digitised polygons of study sites using geographical information systems. Area and perimeter were computed and log transformed. The distance to the nearest neighbour, the sum of distances to the two nearest neighbours, and so on until the sum of distances to the ten nearest neighbours was computed. The variables distance to the 1, 2, 7, 8, 9 and 10 nearest neighbours were log transformed, and the variables distance to the 3, 4 and 5 nearest neighbours were square-root transformed. The area of grassland patches other than the focal, within distances of 1 km, 2 km, and 4 km from the focal patch, was computed and log transformed. The sign was reversed to make these variables express isolation instead of connectance, and they are henceforth called Isolation 1 km, 2 km and 4 km respectively. The isolation measure proposed by Hanski et al. (1994) was computed using the formula:

$$I_i = -\left(\sum_{j}^{m} \exp(-d_{ij}) * A_j\right),$$

where d_{ij} is distance (km) from the focal patch i to patches j to m, and A_j is patch area (ha). The variable was log transformed before the sign was reversed, and is called "Isolation index" henceforth.

In order to take into account any regional spatial structure in the species richness data, the centred and standardised UTM (WGS84 zone 32) easting (x) and northing (y) were used to compute the seven terms of a cubic trend surface as suggested by Borcard et al. (1992): x^2, xy, y^2, x^3, x^2y, xy^2, y^3.

Species subsets

Grassland species also occurring frequently in other habitats were identified in three external data sets: 1) the species lists from the not chosen grassland sites (see above), 2) a data set on ground floor species in deciduous forest in the same region (Graae and Sunde 2000), and 3) data on species from road verges in the island of Sjælland (Hansen and Jensen 1972). The deletion of those species left 106 strict grassland species out of totally 210 species in the analysis. Numbers of all species and grassland specialist species were log transformed prior to analysis.

Furthermore the species richness data were divided into a number of subsets according to species traits regarding longevity and dispersal ability (the resulting numbers of species were subjected to transformation to achieve a better fit to the normal distribution, log: $y' = \log(y + 0.1)$, sqrt: $y' =$ square root y): longevity was scored in two classes, long-lived species (polycarpic perennials; log), short-lived (sqrt). Species were divided into three classes according to seed bank longevity, transient (log), short-term persistent (log), and long-term persistent. Species were divided into four classes according to seed mass, < 0.1 mg (sqrt), seed mass 0.1–1 mg (log), seed mass 1–10 mg (sqrt), seed mass > 10 mg. Dispersal syndrome was initially scored as no dispersal structure (log), and any dispersal structure (log). The latter subset was broken into myrmecochores (with elaiosome), bird-endozoochores (fleshy fruit), epizoochores (awn, hook or burr; sqrt), and anemochores

Table 1. Stepwise multiple linear regression on number of all species (upper panel) and number of specialised grassland species (lower panel) ($m = 85$). R^2 is the coefficient of multiple determination. y, y^2 and y^3 are the northing and its quadratic and cubic functions. Temp^{cal} is the calibrated Ellenberg T-value.

step	variable	sign	p	model R^2
1	Perimeter	+	0.0001	0.5496
2	Habitat heterogeneity	+	0.0007	0.6089
3	y^3	+	0.0006	0.6628
4	Temp^{cal}	÷	0.0014	0.7036
1	Distance to coast	÷	0.0001	0.3310
2	Habitat heterogeneity	+	0.0001	0.4422
3	Temp^{cal}	÷	0.0016	0.5074
4	y	+	0.0016	0.5655
5	Perimeter	+	0.0041	0.6089
6	y^2	÷	0.0061	0.6450

(pappus or wing; log). The dispersal syndrome classes were cross-combined with two classes of seed-bank longevity (transient and short-term persistent vs long term persistent), yielding eight species groups: no dispersal structure and short-lived seed bank (log), no dispersal structure and long-lived seed bank (sqrt), any dispersal structure and short-lived seed bank (sqrt), any dispersal structure and long-lived seed bank (sqrt), epizoochorous and short-lived seed bank, epizoochorous and long-lived seed bank, anemochorous and short-lived seed bank, and anemochorous and long-lived seed bank (sqrt). Information on plant life-span, seed mass, seed/fruit structures presumably adaptations to dispersal, and seed bank longevity, was obtained from literature sources, mainly Hodgson et al. (1995), whose definitions of dispersal syndromes and seed-bank longevity classes were followed. Some additional data were obtained from Lindacher (1995), and from own observations. Throughout the text n denotes the number of species, and m the number of sites.

Data analysis

Inter-correlation among explanatory variables was investigated with Pearson's product moment correlation. To answer questions 1 and 2 (see Introduction) the explanatory variables were included in a regression model using a stepwise procedure (Anon. 1990: proc reg, forward selection) with one species richness variable as dependent variable. All explanatory variables were available in each analysis, but variables were included in a regression model only if their simple regression on the dependent variable was significant at the 5% level, and if their additional explanatory power in a model was significant at the same level. In case of multiple terms the significance level was corrected according to the Bonferroni principle ($0.05/\alpha$ where α is the number of terms in the regression model). In the tables only the sign of the parameter estimate is given since that was constant, while the absolute size was very sensitive to which other terms were included.

To answer question 3 the variables expressing area, isolation, site conditions, and habitat heterogeneity were included in a series of logistic regression models using a stepwise procedure (Anon. 1990: proc logistic, forward selection). Only strict grassland species (see above) with a number of occupied sites above 19 (limit chosen arbitrarily) were included ($n = 42$). To answer question 4 the logarithm of the number of sites occupied by each species was investigated for correlation (Pearson's product moment) with log(seed mass) and with the absolute deviation from the median log(seed mass). The last measure was estimated as the mean over occupied sites of the deviation from median log(seed mass) of species at that site, henceforth called deviation from community median.

Results

Proportions of the variation in species richness explained by area and isolation vs site conditions

A stepwise multiple regression model for species richness (Table 1) had four significant terms, which accounted for 70.4% of the variation. The first term was patch perimeter, which is highly dependent on patch area. The second term indicates an importance of habitat heterogeneity independent of area. These two parameters were not correlated ($\rho = 0.018$, $p = 0.87$). The third term, y^3, reflected a decline in species richness from south to north within the investigation area even for patches of equal size and heterogeneity. The fourth term, Temp^{cal}, indicated an influence of topoclimate on species richness. A similar stepwise regression model for the number of grassland specialist species is also shown in Table 1.

Relative importance of area, isolation and site conditions among groups of species with different traits

Stepwise regression on number of species in different biological groups are presented in Tables 2 and 3. Numbers of short-lived and long-lived species were both explained by perimeter. The number of long-lived species did further increase with heterogeneity and northing (y^3) and decrease with warmness (Temp^{cal}). The number of short-lived species did further decrease with isolation and towards north-east, and increase with Isolation 4 km and soil pH (Table 2).

The number of species within classes of seed-bank longevity did not show differential response to area measures, but the number of species with a short-term persistent seed bank seemed affected (negatively) by isolation. Further, northing (y^3) and inclination contributed to the regression model for species with a transient seed bank, heterogeneity to the model for species with a seed bank, and heterogeneity, warmness (Temp$_{cal}$) and distance to the coast (the last two negatively) for species with a long-term persistent seed bank (Table 2).

The number of species within all classes of seed mass was well explained by area functions. The number of species with very light seeds ($<$ 0.1 mg) seemed to increase the more sandy the soil and to increase with heterogeneity. The number of species with seed mass 0.1–1 mg was also affected by heterogeneity (positively) and by distance to the coast (negatively). Only the number of species with seed weights 1–10 mg was affected by isolation (negatively) and also by inclination (Table 2).

Half of the species had no apparent adaptation for dispersal, and one quarter had apparent adaptations to dispersal with vertebrates. The number of species within all dispersal group was well explained by area functions. Habitat heterogeneity contributed to the regression models for epizoochorous and anemochorous species. The explanatory model for all species with apparent dispersal adaptations consisted of the same terms as the model for the anemochores. Only the epizoochorous species seemed affected (negatively) by

Table 2. Stepwise multiple linear regression on number of species in functional groups: long- and short-lived species, species within classes of seed mass, species within classes of seed bank longevity, and species with contrasting dispersal adaptations (m = 85). R^2 is the coefficient of multiple determination. y, y^2, y^3, and xy are the geographic coordinates and their quadratic and cubic functions. Temp^{cal} is the calibrated Ellenberg T-value. Isolation 4 km is the negative expression of the sum of neighbour grassland area within 4 km radius. Soil type increases from sand to clay.

	step	variable	sign	p	model R^2
	1	Perimeter	+	0.0001	0. 5510
long-lived	2	Heterogeneity	+	0.0006	0.6121
(n = 155)	3	y^3	+	0.0005	0.6664
	4	Temp^{cal}	÷	0.0030	0.7013
	1	Perimeter	+	0.0001	0.3699
short-lived	2	xy	÷	0.0029	0.4347
(n = 55)	3	Isolation 4 km	÷	0.0142	0.4753
	4	pH	+	0.0045	0.5260
transient seed bank	1	Perimeter	+	0.0001	0.5020
(n = 103)	2	y^3	+	0.0018	0.5583
	3	Inclination	+	0.0005	0.6202
short-term persistent	1	Perimeter	+	0.0001	0.4654
seed bank (n = 44)	2	Isolation 4 km	÷	0.0018	0.5295
	3	Heterogeneity	+	0.0010	0.5885
	1	Area	+	0.0001	0.4042
long-term persistent	2	Heterogeneity	+	0.0003	0.4941
seed bank (n = 51)	3	Temp^{cal}	÷	0.0091	0.5352
	4	Distance to coast	÷	0.0073	0.5754
seed mass	1	Perimeter	+	0.0001	0.2040
<0.1mg	2	Soil type	÷	0.0001	0.3680
(n = 30)	3	Heterogeneity	+	0.0003	0.4633
seed mass	1	Area	+	0.0001	0.4961
0.1–1mg	2	Heterogeneity	+	0.0003	0.5694
(n = 82)	3	Distance to coast	÷	0.0005	0.6293
seed mass	1	Perimeter	+	0.0001	0.4232
1–10mg	2	Inclination	+	0.0012	0.4931
(n = 65)	3	Isolation 4 km	÷	0.0004	0.5656
s. mass > 10mg (*n* = 22)	1	Perimeter	+	0.0001	0.4438
pappus or wing	1	Area	+	0.0001	0.3853
(n = 33)	2	y^3	+	0.0002	0.4831
	3	Heterogeneity	+	0.0026	0.5384
fleshy fruit	1	Perimeter	+	0.0001	0.3256
(n = 19)	2	Inclination	+	0.0042	0.3900
awn or burr	1	Perimeter	+	0.0001	0.4101
(n = 44)	2	Isolation 4 km	÷	0.0005	0.4916
	3	Heterogeneity	+	0.0004	0.5662
elaiosome	1	Area	+	0.0001	0.3435
(n = 8)	2	PH	÷	0.0030	0.4108
any dispersal structure	1	Area	+	0.0001	0.5394
(n = 104)	2	y^3	+	0.0007	0.6004
	3	Heterogeneity	+	0.0002	0.6628
no dispersal structure	1	Perimeter	+	0.0001	0.4410
(n = 103)	2	Heterogeneity	+	0.0011	0.5093
	3	Distance to coast	+	0.0039	0.5575

Table 3. Stepwise multiple linear regression on number of species in functional groups: long- and short-lived species, species within classes of seed mass, species within classes of seed bank longevity, and species with contrasting dispersal adaptations ($m = 85$). R^2 is the coefficient of multiple determination. Y is the geographic northing. Temp^{cal} is the calibrated Ellenberg T-value. Isolation 4 km is the negative expression of the sum of neighbour grassland area within 4 km radius. Soil type increases from sand to clay. Radiation eqx is the potential solar radiation at equinox. For myrmecochores and ornithochores one or both seed bank subgroups had to few species to make analysis possible.

	Transient or short-term persistent seed-bank					Long-term persistent seed-bank				
	step	variable	sign	model R^2	p	step n = 6	variable	sign	model R^2	p
	n = 21									
Pappus or Wing	1	Perimeter	+	0.3837	0.0001	1	Isolation index	÷	0.3607	0.0001
	2	Inclination	+	0.5256	0.0001	2	Dist. to coast	÷	0.4614	0.0002
	3	Isolation 4 km	÷	0.6166	0.0001					
	4	PH	+	0.6480	0.0091					
	n = 35					n = 9				
Awn or burr	1	Perimeter	+	0.4632	0.0001	1	Radiation eqx	÷	0.1550	0.0002
	2	Temp^{cal}	÷	0.5002	0.0158	2	Area	+	0.2138	0.0157
Any dispersal structure	n = 81					n = 17				
	1	Perimeter	+	0.4992	0.0001	1	Area	+	0.2735	0.0001
	2	Heterogeneity	+	0.5428	0.0064	2	Soil type	÷	0.3693	0.0007
	3	Isolation 4 km	÷	0.6083	0.0004					
	n = 63					n = 34				
No dispersal structure	1	Perimeter	+	0.4589	0.0001	1	Area	+	0.3708	0.0001
	2	Heterogeneity	+	0.5681	0.0001	2	Heterogeneity	+	0.4736	0.0001
	3	y	+	0.6410	0.0001	3	Temp^{cal}	÷	0.5162	0.0092
	4	Inclination	+	0.6687	0.0116	4	Dist. to coast	÷	0.5666	0.0031

isolation. Further, the number of myrmecochores was related negatively to pH, the number of ornithochores to inclination, and the number of species without any apparent dispersal adaptation to distance to the coast (Table 2).

Separating the dispersal-related groups into groups of short-lived (transient and short-term persistent) and long-lived seed banks showed some differences (Table 3). For the epizoochorous species with a short-lived seed bank area functions contributed strongly to the regression model, much less markedly for those with a long-lived seed bank. Anemochores with a long-lived seed bank were affected negatively by isolation, those with a short-lived seed bank less markedly so. For the latter group area was more important. The two groups of species with any dispersal structure both were affected (positively) by area functions, while those with a short-lived seed bank also by heterogeneity and isolation, and those with a long-lived seed bank by soil type (number increasing the more sandy the soil). The two groups of species with no dispersal structures were rather similar, area and heterogeneity being the most important explanatory variables.

Since mean pH was correlated with perimeter ($\rho = 0.348$, $p = 0.001$, but not with area, $\rho = 0.191$, $p = 0.08$) a set of similar regression models as above were made with pH added first. In all cases this action did not alter the significant terms, or only changed one area measure to another (typically perimeter to area).

The relative importance of area, isolation and site conditions among grassland species

Two thirds of the species had a significant relation to one or more site conditions in the stepwise logistic regression of species presences, most of them to mean soil pH (Table 4). Five species had negative relationships with the soil type classification, which means that they occur predominantly on sandy soils. Eleven species occurred predominantly near the coast, and one predominantly on inland sites. One quarter of the species had a positive relation to a measure of habitat heterogeneity, and only one a negative relation (to number of soil types). Nine species occurred predominantly on large sites, while two species occurred mostly on small sites. Twelve species had a significant relation to an isolation measure, in most cases to Isolation 4 km. Only one of these species, *Potentilla erecta* (L.) Räusch., had a positive relationship to isolation (distance to the two nearest neighbours).

The regional abundance of species as explained by deviation in seed mass from the community median

No correlation was found between log(seed mass) and regional abundance (number of sites occupied), but there was a marginally significant linear correlation with log(regional abundance) ($\rho = 0.1299$; $p = 0.0622$).

Table 4. Stepwise logistic regression of presence of strict grassland species with a regional abundance ≥ 20 sites. Only the sign of the parameter estimate and its significance is shown in the table. $^{*}0.05/\alpha \geq p > 0.01/\alpha$, $^{**}0.01/\alpha \geq p > 0.001/\alpha$, $^{***}0.001/\alpha \geq p$, where α is the number of terms in the regression model. Radiation eqx is the potential solar radiation at equinox. Soil type increases from sand to clay. Dist X neighb is the sum of distances to the number of neighbours indicated by the value of X. Isolation 1 km and 4 km are the negative expressions of the sum of neighbour grassland area within 1 and 4 km radii respectively.

Species	No. sites	Soil pH	Inclination	Radiation eqx	Mean soil type	Dist. to coast	Habitat het.	No. soil types	Area	Perimeter	Isolation index	X	Dist X neighb	Isolation 1 km	Isolation 4 km
Agrostis vinealis Schreb.	34								+***			10	÷*		
Aira praecox L.	31														÷***
Anthyllis vulneraria L.	20			÷*							÷***				
Arabis hirsuta (L.) Scop.	29		+***												
Arenaria serpyllifolia L.	39	+***					+**								
Armeria maritima (Mill.) Willd.	23					÷***									÷***
Artemisia campestris L.	41					÷***						4	÷*		
Avenula pratensis (L.) Dumort.	55					÷**									
Briza media L.	24	+***							+**						
Calluna vulgaris (L.) Hull	24				÷**		+*								
Carex caryophyllea Latourr.	28									+***					
Cerastium semidecandrum L.	46					÷***									
Cirsium acaule Scop.	25							+ ***		+**					
Danthonia decumbens (L.) DC.	22	÷*	+**						+***						
Festuca ovina L.	38				÷*				+***						
Festuca trachyphylla (Hack.) Krajina	20														÷***
Filipendula vulgaris Moench	53						+**								
Hieracium umbellatum L.	29							÷ **							
Jasione montana L.	20				÷*										÷***
Lathyrus montanus Bernh.	21			÷**											
Luzula campestris (L.) DC.	50								+***						
Lychnis viscaria L.	36				÷*					÷ **					
Myosotis ramosissima Rochel	25	÷*				÷**									
Ononis repens L.	54		+***			÷*									
Phleum phleoides (L.) H.Karst.	22			+*		÷*	+*					4	÷**		
Phleum pratense L. ssp. bertolonii (DC.) Bornm.	43		+***			÷**									
Pimpinella saxifraga L.	43														
Plantago media L.	23	+***				÷***									
Potentilla argentea L.	23						+***								
Potentilla erecta (L.) Räusch.	25			÷*								2	+**		
Potentilla heptaphylla L.	25	+*					+**							÷***	
Primula veris L.	31	+*		÷**								1	÷*		
Pulsatilla pratensis (L.) Mill.	22				÷**	÷***	+*								
Rumex acetosella L.	43	÷**												÷**	
Saxifraga granulata L.	39			÷*											÷**
Sedum acre L.	32			+*		÷***	+**								
Senecio jacobaea L.	24	+**													
Solidago virgaurea L.	31						+*			÷**					
Stellaria graminea L.	50	÷***		÷*		+*									
Thymus pulegioides L.	22	+*								+***					
Viola canina L.	49	÷***								+*					

There was a linear correlation between deviation from community median and log(regional abundance) which was significant ($p = 0.0402$) but with a low explanatory power ($\rho = 0.1428$). When the species were divided into strict grassland species and species found in other habitats as well, these patterns were found only for the latter group.

Discussion

Semi-natural grasslands in Denmark are inhabited by a group of plant species which is not easy to distinguish from groups of species with preference for other habitats. Some species of meadows and forests are sometimes found in moist grassland. The commoner grassland species tend to occur also in these habitats, and furthermore in improved grasslands and on road banks. This feature makes Danish grassland patches sub-optimal for studies contributing to the construction of a theory of metacommunities (e.g. Harrison 1999). On the other hand most plant communities in the world share a large proportion of their species with other communities.

Not all the explanatory variables used in the regression modelling are easily interpretable in the context of species richness. Patch perimeter, for example, must evidently be correlated with patch area. The better fit to species richness of perimeter is probably due to the fact that many large and species-rich sites are Litorina-time coastal slopes. The reason for the different behaviour of area and perimeter, is that, though strongly and positively correlated, the relation between them vary with patch shape. Small burial mounds have a rounded shape (small area:perimeter relation) and a relatively acid soil, and large sites on steep coastal slopes are long and narrow (large area:perimeter relation) and have an unleached and often neutral-alkaline soil.

A strong south to north cline in species richness was found. Northing, y, and more frequently its cubic function, y^3, correlates with a gradient in percentage land area covered by grassland, and a weak gradient in local climate and predominating soil type. These are not inseparable from landscape history, since the nature and intensity of land-use were dependent on climate, soil and topography, and since land-use may have influenced soil development. There is roughly one third of the variation in species richness left unexplained by area, isolation and site conditions. There was hardly any difference in productivity among sites, at least the calibrated Ellenberg N-value was barely without variation. Also climate is almost constant throughout the study area. It is likely that land-use history can explain some of the residual variation in species richness (Bruun et al. unpubl.). But such a relationship is difficult to reveal since archival sources from Denmark almost exclusively deal with a larger spatial scale than that of particular sites. The finding of Pärtel and Zobel (1999) that the local species richness in alvar grasslands of Estonia increases with site ages from 600 to 6000 yr makes it reasonable to expect a relationship between diversity and landscape history also in the system described here.

Patch area and patch habitat heterogeneity seem to play the largest role in explaining the species richness of the studied grasslands. When only small sites are dealt with, isolation plays a significant role. This pattern has been shown in a number of studies on fragments of ancient woodland in northern Europe (Peterken and Game 1984, Dzwonko and Loster 1989, Zacharias and Brandes 1990, Grashof-Bokdam 1997, Honnay et al. 1999). It has to my knowledge not been shown before in patches of grassland within the same region. On the contrary, Eriksson et al. (1995) found no relationship between species richness and area or isolation. This may indicate that Danish grasslands have been fragmented for a very long time compared to the central Swedish. Many of the Bronze Age burial mounds supporting grassland vegetation in this study are situated close to villages founded in the early Medieval times or earlier, and they have been surrounded by arable fields for as long.

For the set of strict grassland species the distance to the coast seems to be important. This variable is not easily interpretable. The climate is probably only slightly different on the inlet coast than a few kilometres inland, and the influence of salt spray is probably negligible since the wind only has the opportunity to pass over 1–10 km of water surface and the water is brackish. Steep slopes of relatively unleached soils occur, however, predominantly along the coast line, and they probably have a very long continuity as permanent pasture.

No difference between long-lived and short-lived species was found regarding patch area. The negative effect of isolation on the number of short-lived species could be interpreted as a difficulty to re-colonise small and isolated sites once extinct.

For all three groups of species with differing seed bank longevity patch area (or perimeter) was included as the first term in the regression models. But the coefficient of determination was decreasing from species with transient to species with long-term persistent seed banks, indicating less dependence on area the longer the life-span of seed banks.

Seed mass seems to be a poor predictor of dispersal ability in this study. Species with seed mass 1–10 mg was affected by isolation, but contrary to the expected not those with heavier seeds. Area (or perimeter) was the best predictor of species richness for all groups, but with relatively low predictive power for the species with seed mass < 0.1 mg.

The finding that species adapted to ant dispersal and species with no apparent dispersal adaptation are not limited by isolation is somewhat surprising. Even more so is the finding that species with adaptation to epizoochory constitute the most isolation-limited group. These results put a serious question mark on the value of dispersability inferred from primary dispersal adaptation as deduced mainly from dispersule morphology. Especially dispersal by large herbivores, either in the fur or though the guts, is probably important in the investigated grasslands, and has even been much more important in the open field system prevailing in Denmark until the enclose movement 200 yr ago (Bruun and Fritzbøger unpubl.). For example all alleged myrmecochorous species in this study also have the ability to survive passage though the digestive tract of some animals (*Carex pilulifera* L. in cattle, sheep, red deer and hare; *Cytisus scoparius* (L.) Link in sheep; *Danthonia decumbens* (L.) DC. in cattle and sheep; *Polygala* sp. and *Viola* spp. in cattle (Welch 1985); *Luzula campestris* in cattle (Stender et al. 1997)). These animals could potentially act as occasional long-distance dispersal vectors.

The cross-combination of dispersal syndrome and seed-bank longevity did generally not show the expected trends. Area was not more important to species with short-lived seed banks, with exception of the epizoochorous species. Isolation was associated with dispersal syndrome groups in the opposite way of that expected. Anemochores seemed more affected by isolation than the other groups. This may be explained by the conception that wind dispersal is more wasteful than other dispersal modes (Salisbury 1976). Another possible explanation for the lack of clear pattern is that at least relatively dry grassland patches have a significant contingent of species that can occur as arable weeds. These have typically long-lived seed banks, and they prevail in small patches due to border effects, and they are not affected by isolation.

Many single species showed one or more significant relationships to the parameters (Table 4). The range of soil pH over all sites was 4.5–8.4. The lower value corresponds to the limit above which the solubility of free reactive aluminium is very low (Tyler 1996). Therefore "acidifugous" species (sensitive to free Al) should potentially be able to grow in all sites, which was obviously not the case. Likewise, calcifugous species should be absent from sites only with soil pH > 7. The pattern that quite many species would seem to prefer sites with high soil pH, and relatively few would prefer sites with low soil pH, was therefore expected. The same line of thinking could be used with preference for sandy vs clayey soils.

An explanation for the pattern that many species seem to prefer sites with high habitat heterogeneity or number of soil types is less straightforward to explain. The same was reported in a similar study by Eriksson et al. (1995). It appears, however, from the table that it is generally species with a broad ecological amplitude with respect to soil acidity or soil moisture or both. Examples are *Sedum acre* L. and *Cerastium semidecandrum* L. which are found in dry sites irrespective of soil pH, and *Solidago virgaurea* L. and *Succisa pratensis* Moench which occur along the entire pH range found in the studied sites and under various moisture conditions. One potential explanation would then be that such species build up larger populations in heterogeneous sites and then will be less susceptible to local extinction due to extreme climatic events compared to homogeneous sites.

Twelve species had a negative relationship to isolation. The results suggest that these species are dispersal limited, and this hypothesis could be subjected to testing experimentally. The positive relationship of *Potentilla erecta* to isolation is a reflection of its preference for the damp north-facing side of burial mounds. At the same time the result suggests tentatively that the species is very persistent, since its dispersability is presumably low in a fragmented landscape.

The seed mass, and its deviation from the community median, was not a good predictor of the regional abundance of species. The result is not in good accordance with the heuristic model developed by Eriksson and Jakobsson (1998). Among the strict grassland species no systematic relationship between seed mass and regional abundance was found. Only for species found also in other semi-natural habitats the findings were partially consistent with this model. Eriksson and Jakobsson (1998) did, however, only find support for their model using phylogenetically independent contrasts (Harvey and Pagel 1991), not correlations over all species.

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