

Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands

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Abstract

Habitat fragmentation of semi-natural habitats is a serious problem in nature conservation because it leads to a decrease in habitat area and an increase of the isolation of habitat islands. In this paper, we examined the effects of habitat fragmentation on species richness and assemblages of four taxonomic groups. First, we used species-area relationships to assess the effect of habitat area on species richness per habitat island. Second, cumulative species-area curves were used to assess the question whether large habitat islands contain more species than several small islands of the same total area. Third, we examined to what extent species assemblages of species-poor habitat islands are nested subsets of those of species-rich ones.

We analysed presence-absence data of vascular plants and bryophytes in 36, and of day-active butterflies and grasshoppers in a subset of 23 habitat islands (montane calcareous fens). The species-area relationship of each group was positive but was highly significant only for vascular plants. The slopes of the relationship on the log-log-scale were rather low (z -values: 0.06–0.11). The cumulative species-area curves of all groups showed that a set of small habitat islands contained more species than a set of a few large habitat islands with the same total area. The results of our nestedness analyses depended on the underlying null models of the test statistics. Applying the method of Wright & Reeves (1992), all groups were significantly nested within the archipelago of habitat islands. Yet, using the method of Brualdi & Sanderson (1999), none of the groups showed non-random patterns. Our study showed that species richness increased with the area of habitat islands, but overlap among them was so low that even small habitat islands contributed to overall species richness. Therefore, a mosaic of several wetland islands, including small ones, is necessary to maintain species diversity at the landscape level.

Die Fragmentierung naturnaher Habitats ist ein Problem im Naturschutz, weil sie einerseits eine Verkleinerung der Gesamtfläche und andererseits die Isolation der entstehenden Habitatsinseln bewirkt. In diesem Artikel untersuchen wir die Effekte der Fragmentierung von Feuchtgebieten auf die Anzahl und Zusammensetzung der Arten von vier taxonomischen Gruppen. Erstens beschreiben wir den Effekt der Habitatsgröße auf die Artenzahl pro Habitatsinsel. Zweitens konstruieren wir kumulative Artenzahl-Areal-Kurven, um zu entscheiden, ob mehrere kleine Habitatsinseln mehr oder weniger Arten enthalten als wenige große Habitatsinseln mit der gleichen Gesamtfläche. Drittens gehen wir der Frage nach, in welchem Ausmaß artenarme Habitatsinseln nur eine Teilmenge aus der Menge an Arten von artenreichen Inseln enthalten ('Nestedness'-Frage). Wir analysierten Präsenz-Absenz-Daten von Gefäßpflanzen und Moosen in 36 bzw. von Schmetterlingen und Heuschrecken in 23 montanen Kalkflachmooren. Die vier Gruppen zeigten alle eine positive

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Artenzahl-Areal-Beziehung, die aber nur bei den Gefäßpflanzen hoch signifikant war. Die Steigung der Artenzahl-Areal-Beziehungen in doppelt-logarithmischer Darstellung war jedoch bei allen Gruppen relativ klein (z -Werte: 0,06–0,11). Die kumulativen Artenzahl-Areal-Kurven zeigten für alle Gruppen, dass mehrere kleine Habitatsinseln mehr Arten enthielten als wenige große Inseln mit der gleichen Gesamtfläche.

Die Resultate der Nestedness-Analyse hingen vom verwendeten Nullmodell für die Teststatistik ab. Wurde die Methode von Wright & Reeves (1992) verwendet, so konnten bei allen Gruppen signifikante Nestedness festgestellt werden. Wurde hingegen die Methode von Brualdi & Sanderson (1999) verwendet, konnten bei keiner Gruppe signifikante Muster gefunden werden. Unsere Untersuchungen zeigten, dass zwar die Artenzahlen mit der Größe der Habitatsinseln zunahmen, dass aber auch selbst kleine Inseln wesentlich zur Gesamtartenzahl beitrugen. Ein Mosaik aus großen und kleinen Habitatsinseln ist deshalb nötig, um die Artenvielfalt auf Landschaftsniveau zu erhalten.

Key words: bryophytes – butterflies – calcareous fens – grasshoppers – habitat fragmentation – nested subset – saturation function – SLOSS – vascular plants

Introduction

In Central Europe, the total area of natural and semi-natural habitats has been dramatically reduced by modern land-use and urban development. As a result, formerly large and continuous habitats have become fragmented, implying decreased habitat area and formation of many habitat islands (Saunders et al. 1991). The increase of species richness (number of species per habitat island) with the area of habitat islands has been described by the power law $S = cA^z$, where S is the species richness of a habitat island, A is its area, and c and z are constants (Preston 1962, MacArthur & Wilson 1967). This relationship suggests that large nature reserves should have high conservation priority.

However, the simple species-area relationship does not make predictions about the distribution patterns of species among habitat islands and, thus, about the total species richness of an archipelago consisting for example of many small or a few large islands. This problem has been discussed intensively in the SLOSS debate (single large or several small nature reserves). Wilson & Willis (1975) and Diamond & May (1976) suggested that single large reserves often contain more species than a collection of small reserves. On the other hand, Simberloff & Abele (1976) argued that the theory of island biogeography of MacArthur & Wilson (1967) is neutral with respect to the SLOSS question. If species overlap among islands is small, then many small islands should together contain a greater number of species than a single large island of the same total area. In fact, empirical studies support the latter idea (Quinn & Harrison 1988, Virolainen et al. 1998). Tscharrntke et al. (2002) even argue that small habitat fragments deserve more attention in conservation than recent publications suggest.

Recently, the concept of nestedness has been proposed to solve the SLOSS question (Worthen 1996). Nestedness occurs when a species assemblage on a species-poor island is a subset of the species assemblage on a species-rich island (Patterson & Atmar 1986). If communities are strongly nested, then a collection of small habitats will contain a smaller number of species than a single large habitat of the same total area. Evidently, this is only true when species richness per habitat island also strongly increases with habitat area.

Furthermore, effects of habitat fragmentation may differ among taxonomic groups. Only few studies examine more than one group within the same archipelago of habitat islands, and studies are biased towards 'popular groups' such as birds and mammals (see Bonnet et al. 2002).

The scope of this paper is to examine the species-area relationship, the SLOSS question and nestedness of four taxonomic groups (vascular plants, bryophytes, day-active butterflies and grasshoppers) in fragmented montane wetlands (calcareous fens) in Switzerland. The investigated habitat type is species-rich, but highly fragmented because in Switzerland roughly 90% of the total wetland area has been destroyed since 1850 (BUWAL 1990). In detail, we address the following questions for the four taxonomic groups:

- (1) Does species richness increase with habitat area?
- (2) Is species richness positively correlated between pairs of taxonomic groups?
- (3) Do large habitat islands contain more species than a collection of several small islands of the same total area?
- (4) To which degree are the species assemblages in species-poor habitat islands subsets of those in species-rich habitat islands?

Materials and Methods

Field studies

We investigated habitat islands of montane calcareous fen meadows in the pre-Alps of Switzerland. These extensively used wet grassland communities of the *Carrion davallianae* alliance (Ellenberg 1996) are maintained either by late-season mowing or by cattle grazing. Annual rainfall is high (1500–2800 mm, Uttinger 1967). Bedrock is mainly composed of various calcareous sediments of tertiary and mesozoic age (Spicher 1972). The soil of these sites is nutrient-poor but base-rich and aboveground plant biomass is low (Bergamini et al. 2001a, Pauli et al. 2002).

We randomly selected 36 habitat islands from a set of over 300 listed in a national inventory (BUWAL 1990). The selection was stratified into two management practices (mown vs. grazed) and three altitudinal classes (800–1000 m, 1000–1200 m, and 1200–1400 m a. s. l.) to guarantee a representative sample of calcareous fens. The areas of the selected habitat islands were obtained from the inventory (BUWAL 1990) and ranged from 0.9–18.5 ha. A two-way ANOVA showed that habitat area did not vary among the management ($F_{1,32} = 1.17$, $p = 0.29$) and altitudinal classes ($F_{2,32} = 0.15$, $p > 0.5$).

The presence or absence of vascular plants and bryophytes was recorded in all 36 habitat islands (Table 1). The number of vascular plant species in each habitat island was obtained by intensive searches in May and July/September 1995. In addition, species identity was recorded in five randomly arranged 2-m² plots within each habitat island (Peintinger 1999). Bryophytes (mostly mosses) were studied with the same sampling design, but fieldwork was conducted only once per habitat island between May and July 1997 (Bergamini et al. 2001b).

Since data collection for insects was more time-consuming than for plants, the presence-absence of day-active butterflies and grasshoppers was recorded in 24 habitat islands (Wettstein & Schmid 1999); with one exception, these were a subset of the 36 habitat islands (Table 1). Habitat area of the subset ranged from 0.9 to 15.5 ha. A two-way ANOVA showed that habitat area of this subset again did not vary among the management ($F_{1,20} = 0.37$, $p > 0.5$) and altitudinal classes ($F_{2,20} = 0.32$, $p > 0.5$).

At each site data of species richness of butterflies were collected during a first visit from 4 June to 18 July 1996 and during a second visit from 19 July to 26 August 1996. Grasshoppers were recorded between 28 July and 17 September 1996 (see Wettstein & Schmid 1999). These visits are sufficient to record almost all grasshopper and most of the butterfly species

(W. Wettstein, pers. comm.). We were not able to conduct further visits since data collection was constrained by the number of habitat islands. Because of bad weather conditions, data could not be obtained for one habitat island. Thus, for butterflies and grasshoppers only 23 habitat islands were included in the analyses.

Presence-absence data of the four taxonomic groups are available from the corresponding author upon request.

Analysis

To assess the effect of habitat area on species richness, we calculated linear regressions using the log-transformed power function $\log_{10}S = \log_{10}C + z \log_{10}A$. Fitting an exponential function to the data (Connor & McCoy 1979) did not yield better results. To examine the pairwise relationships of species richnesses between the four taxonomic groups, a Pearson correlation matrix was used. Correlation coefficients were calculated for each pair of taxonomic groups separately to minimise the effects of missing values.

To investigate the SLOSS-question, we used the cumulative species-area curves (= saturation functions) as proposed by Quinn & Harrison (1988). We plotted cumulative species richness against cumulative habitat island area. The shape of the curve depends on the sequence of the habitat area: the habitat islands were ranked by their area in ascending (curve 1) or in descending (curve 2) order. If curve (1) lies above curve (2), sets of large habitat islands contain less species than sets of smaller habitat islands of the same total area. The SLOSS index (= saturation index) of Quinn & Harrison (1988) was calculated to compare the cumulative species-area curves for the four taxonomic groups. This index is defined as the quotient of the area under curve (1) and the area under curve (2). The index is > 1 if several small habitat islands contain more species than a few large ones with the same total habitat area and < 1 if the opposite is true.

For the analysis of nestedness, we constructed incidence matrices using 0 for absence and 1 for presence. Then, islands (rows) were ranked in terms of decreasing species richness, and species (columns) were ranked in terms of decreasing numbers of occupied islands (= incidence). If a community is perfectly nested, the re-arranged presence-absence matrix is triangular with the 1s clustering in the upper left corner. We used two different metrics to quantify nestedness, (1) the C metric of Wright & Reeves (1992) and (2) the recently introduced 'discrepancy' of Brualdi & Sander (1999). For the C metric it is first necessary to calculate N_c , that is the number of times that a species' presence at a site correctly predicts its presence at a

richer site across species and sites. The metric N_c increases with increasing nestedness, but has also a tendency to be larger for large matrices as compared with small ones. Therefore, the standardised index C was calculated

$$C = \frac{N_c - \{EN_c\}}{\max\{N_c\} - \{EN_c\}},$$

where $\max\{N_c\}$ is the value of N_c under perfect nesting with a given number of habitat islands and species,

and $E\{N_c\}$ is the expected value of N_c under the null hypothesis that all species are independently and with equal probability distributed over the islands (Wright & Reeves 1992). That is, species incidence (row sum) is allowed to vary among islands whereas species richness (column sum) is fixed. $E\{N_c\}$ can be calculated analytically because simulations have shown that the metric N_c is approximately normally distributed under the mentioned null model. Therefore, after a z-transformation simple significance tests are possible (Wright & Reeves 1992).

Table 1. Location, habitat area, and investigated taxonomic groups in 36 habitat islands (calcareous fens)

No.	Municipality (canton)	Physiographic unit	Longitude (east)	Latitude (north)	Area (ha)	Investigated taxonomic group			
						Vasc.	Bryo.	Butter.	Grass.
3243	Illgau (SZ)	ANI	8°45'09"	47°59'57"	18.51	x	x	–	–
1555	Reichenburg (SZ)	ANI	8°58'11"	47°08'47"	18.01	x	x	–	–
597	Ebnat-Kappel (SG)	ANT	9°07'35"	47°11'60"	15.46	x	x	(x)	(x)
1141a	Einsiedeln (SZ)	ANI	8°48'09"	47°08'43"	15.30	x	x	x	x
2344	Vorderthal (SZ)	ANI	8°51'04"	47°07'33"	14.05	x	x	x	x
1550	Schübelbach (SZ)	ANI	8°58'04"	47°08'26"	13.38	x	x	x	x
1141b	Einsiedeln (SZ)	ANI	8°48'16"	47°08'43"	10.80	–	–	x	x
3211	Unteriberg (SZ)	ANI	8°49'47"	47°03'42"	9.26	x	x	x	x
3173	Schwyz (SZ)	ANI	8°39'02"	47°03'50"	9.09	x	x	x	x
627	Mollis (GL)	ANG	9°05'16"	47°06'28"	9.06	x	x	–	–
2345	Einsiedeln (SZ)	ANI	8°48'42"	47°08'08"	8.64	x	x	x	x
3144	Rothenthurm (SZ)	ANI	8°42'26"	47°04'54"	7.99	x	x	–	–
2295	Feusisberg (SZ)	ANI	8°43'29"	47°09'49"	7.03	x	x	x	x
607	Nesslau (SG)	ANT	9°10'02"	47°12'25"	6.53	x	x	x	x
543	Wildhaus (SG)	ANT	9°23'37"	47°12'29"	6.01	x	x	–	–
582	Mels (SG)	ANG	9°21'59"	47°02'56"	5.73	x	x	–	–
145	Urnäsch (AR)	ANI	9°18'06"	47°18'57"	4.65	x	x	–	–
556	Grabs (SG)	ANT	9°22'32"	47°09'48"	4.61	x	x	x	x
2899	Rothenthurm (SZ)	ANI	8°42'12"	47°07'31"	4.22	x	x	–	–
874	Hemberg (SG)	MIR	9°09'19"	47°18'07"	3.82	x	x	–	–
1544	Vorderthal (SZ)	ANI	8°55'03"	47°07'42"	3.77	x	x	x	x
3227	Alpthal (SZ)	ANI	8°42'53"	47°02'31"	3.35	x	x	x	x
3181	Sattel (SZ)	ANI	8°38'32"	47°04'15"	2.74	x	x	x	x
3161	Einsiedeln (SZ)	ANI	8°46'30"	47°05'12"	2.52	x	x	x	x
541	Gams (SG)	ANT	9°24'18"	47°12'38"	2.49	x	x	x	x
890	Urnäsch (AR)	ANT	9°14'11"	47°18'24"	2.38	x	x	x	x
1554	Innerthal (SZ)	ANI	8°57'09"	47°06'36"	1.91	x	x	–	–
1904	Quarten (SG)	ANG	9°14'40"	47°05'15"	1.73	x	x	–	–
592	Vilters (SG)	ANG	9°24'44"	47°00'53"	1.54	x	x	–	–
1543	Vorderthal (SZ)	ANI	8°53'37"	47°07'13"	1.42	x	x	x	x
916	Ebnat-Kappel (SG)	ANT	9°07'56"	47°12'32"	1.24	x	x	x	x
2337	Einsiedeln (SZ)	ANI	8°44'41"	47°06'48"	1.23	x	x	x	x
1925	Flums (SG)	ANG	9°16'28"	47°03'09"	1.20	x	x	x	x
902	Ebnat-Kappel (SG)	ANT	9°06'04"	47°15'13"	1.17	x	x	x	x
103	Gais (AR)	ANT	9°28'14"	47°22'57"	1.10	x	x	–	–
3235	Oberiberg (SZ)	ANI	8°45'19"	47°01'36"	1.01	x	x	x	x
3183	Sattel (SZ)	ANI	8°38'41"	47°04'39"	0.87	x	x	x	x

Abbreviations

No.: Code number according to the inventory of fens (BUWAL 1990);

cantons: AR: Appenzell Ausserrhoden, GL: Glarus, SG: St. Gallen, SZ: Schwyz;

physiographic units (sensu Gutersohn 1978): ANI: Innerschweizer Alpen, ANG: Glarner Alpen, ANT: Thur-Alpen, MIR: Rhein-Thur-Gebiet (Mittelland);

investigated taxonomic groups: Vasc.: vascular plants, Bryo.: bryophytes, Butter.: day-active butterflies, Grass.: grasshoppers;

x: investigated habitat islands; (x): site excluded because of bad monitoring conditions.

The discrepancy of Brualdi & Sanderson (1999) is defined as the number of 1s (presence) in an incidence matrix A that must be shifted to produce a perfectly nested matrix. Previously used metrics did not generate any 'gaps' if islands have the same number of species but a different species composition. The nestedness index, N_a , is then calculated as

$$N_a = \frac{(d[A] - E[d])}{SD[d]}$$

where $d[A]$ is the discrepancy of the matrix A, $E[d]$ is the expected number of discrepancies over the entire class of matrices with the same row and column sums as in the original matrix A, and $SD[d]$ is the standard deviation of the resulting distribution of discrepancies. In practice, $E[d]$ and $SD[d]$ were estimated by generating null matrices that were constructed by a recursive backtracking method (Sanderson et al. 1998). One-tailed significance was calculated as the number of null matrices with a discrepancy less than that of the real matrix divided by the total number of constructed null matrices.

In contrast to Wright & Reeves (1992), who only kept column sums constant to generate null matrices (and, hence, to calculate $E\{N_c\}$), Brualdi & Sanderson (1999) kept both row and column sums constant. Thus, the null space (set of matrices generated from a sample space by some random algorithm) of Brualdi & Sanderson (1999) is much more restricted than that of Wright & Reeves (1992).

For the calculations of the regression analyses, the C metrics, and the correlations we used the statistical programming language GENSTAT 5, Release 3 (Payne et al. 1993). The number of discrepancies (N_a metric) was calculated with a program written in MacPerl, Version 5.20. One thousand null matrices were generated using a programme written in APL (Sanderson et al. 1998). Because of the high number of vascular plant species construction of their null matrices was computation-intensive. Therefore, only 400 null matrices were constructed. There were no duplicates in any of the generated sets of null matrices (R.G. Selfridge, pers. comm.).

Table 2. Pearson correlation coefficients for species richness of vascular plants (n = 36), bryophytes (n = 36), day-active butterflies (n = 23), and grasshoppers (n = 23)

	Vascular plants	Bryophytes	Butterflies
Bryophytes	-0.014		
Butterflies	0.451	-0.116	
Grasshoppers	0.142	0.093	0.279

Bold: correlation significant at $p < 0.05$

Results

In total we found 316 vascular plant species, 126 bryophyte species, 64 day-active butterfly species, and 16 grasshopper species. The average species richness per habitat island was 104.8, 33.0, 20.5, and 7.5, respectively. The vascular plant species richness was positively correlated with the species richness of butterflies (Table 2, $p < 0.05$). There were no significant correlations, either positive or negative, between any other pair of taxonomic groups (Table 2).

The relationship between species richness and habitat area (power function) was positive for all taxonomic groups (Fig. 1). However, the slope of the power function was only significantly different from zero for vascular plants ($p < 0.001$) and for butterflies ($p < 0.05$). The relationships for bryophytes and grasshoppers were marginally significant (Table 3).

For all four taxonomic groups, the ascending cumulative species-area curves were lying above the descending curves (Fig. 2). This means that a sampling strategy starting with small habitat islands yielded more species at an intermediate total area than a sampling strategy starting with large islands. The SLOSS index varied between 1.15 and 1.49 and was lowest for grasshoppers and highest for butterflies (Table 3).

Using the metric of Wright & Reeves (1992), the communities of all four taxonomic groups showed sig-

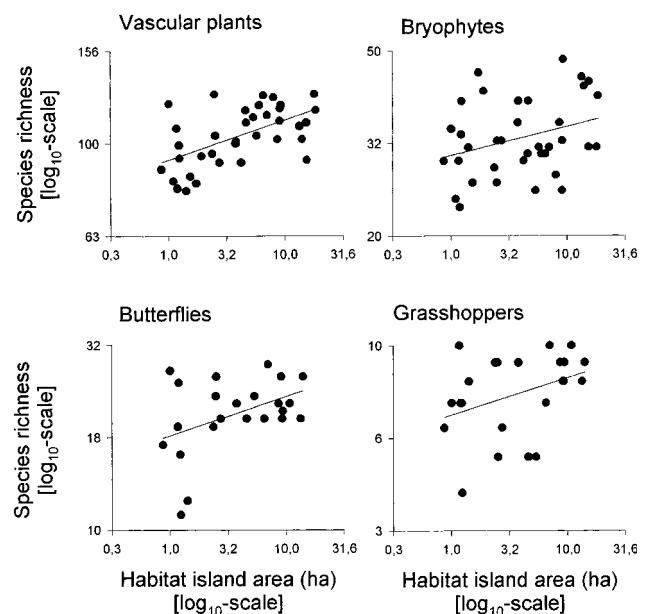


Fig. 1. The relationship between species richness and the area of wetland habitat islands for four taxonomic groups (n = 36 for vascular plants and bryophytes, n = 23 for day-active butterflies and grasshoppers).

nificantly nested subset patterns ($p < 0.001$, Table 3). The standardised metric for nestedness, C , was similar for all four groups. The values were highest for grasshoppers ($C = 0.58$) and lowest for butterflies ($C = 0.49$).

The N_a metric by Brualdi & Sanderson (1999), on the other hand, revealed no significant pattern for any of the examined groups (Table 3).

Discussion

Species-area relationship

We demonstrated that species richness of all four groups was positively related to habitat area. This result is consistent with the classical theory of island biogeography (Preston 1962, MacArthur & Wilson 1967). For vascular plants several studies demonstrate empirically a positive relationship for habitat islands (for wetlands e.g., Findlay & Houlihan 1997, Rey Benayas et al. 1999). For bryophytes only few previous studies exist, but two of these (Tangney et al. 1990,

Nakanishi 2001) reported stronger relationships between species richness and area of real islands than those we found for our habitat islands. Similar to our study, Kimmerer & Driscoll (2000) failed to find a relationship between bryophyte species richness and area of habitat islands. For insects, a positive species-area relationship has repeatedly been reported for both real and habitat islands or patch size of host plants (Connor & McCoy 1979, Rigby & Lawton 1981, Zabel & Tschardtke 1998, Kruess & Tschardtke 2000).

Connor & McCoy (1979) showed that the empirical z -values can range between -0.28 and 1.13 and our estimates are within this range (0.06 – 0.11). A theoretically derived z -value for real islands is 0.26 (Preston 1962, MacArthur & Wilson 1967). The low z -values of habitat islands may be due to a number of causes discussed in the following:

(1) The habitat may have become fragmented only recently and extinction processes in the resulting habitat islands may be delayed (see e.g. Watson 2002). In this case, small habitat islands may be overly rich in species, depressing the slope parameter (MacArthur & Wilson 1967).

(2) The habitat area may have been confounded with other factors that counteracted the positive area effect on species richness. For example, a small habitat island may accumulate more visiting species from adjacent different habitats, be more often managed in a richness-enhancing way, occur at lower altitude with generally larger richness, or be separated by a smaller distance to other islands compared with a large habitat island. In our study neither management nor altitude were confounded with habitat area and distance had no significant effect on species richness of any of the taxonomic groups ($p > 0.05$ for all taxonomic groups). Thus, only the first of the listed factors could have played a certain role (see Wettstein & Schmid 1999).

(3) The habitat islands may not have been true habitat islands for the species assemblages either because some of their members could

Table 3. Species number, slope of the species-area relationship, SLOSS-index and nestedness metrics for vascular plants, bryophytes, day-active butterflies and grasshoppers in habitats islands of wet grasslands (for details see method section)

	Vascular plants	Bryophytes	Butterflies	Grasshoppers
Number of species	316	126	64	16
Number of habitat islands	36	36	23	23
Species-area relationship ($\log_{10}S = \log_{10}c + z \log_{10}A$)				
Intercept ($\log_{10}c$) \pm SE	1.964 \pm 0.016	1.474 \pm 0.024	1.255 \pm 0.034	0.813 \pm 0.039
Slope (z) \pm SE	0.086 \pm 0.022	0.062 \pm 0.033	0.106 \pm 0.050	0.100 \pm 0.057
F-value	15.79	3.51	4.46	3.15
Significance	$p < 0.001$	$p = 0.07$	$p < 0.05$	$p = 0.09$
r^2	0.297	0.067	0.136	0.089
Habitat subdivision				
SLOSS-index	1.34	1.35	1.49	1.15
Nestedness				
Metric of Wright & Reeves (1992)				
N_c	42013	12662	3233	1367
C	0.526	0.553	0.491	0.577
$E(N_c)$	21968	5448	1815	958
max N_c	60087	18499	4704	1667
var N_c	9547	2913	770	244
z -value	205.1	133.6	51.1	26.2
Significance	$p < 0.001$	$p < 0.001$	$p < 0.001$	$p < 0.001$
Metric of Brualdi & Sanderson (1999)				
N_a	1.505	1.087	0.045	0.082
$d(A)$	948	313	133	35
$E[d]$	928.0	303.9	129.0	34.8
$SD[d]$	13.25	8.42	4.27	2.54
No. of iterations (null matrices)	400	1000	1000	1000
Significance	$p > 0.05$	$p > 0.05$	$p > 0.05$	$p > 0.05$

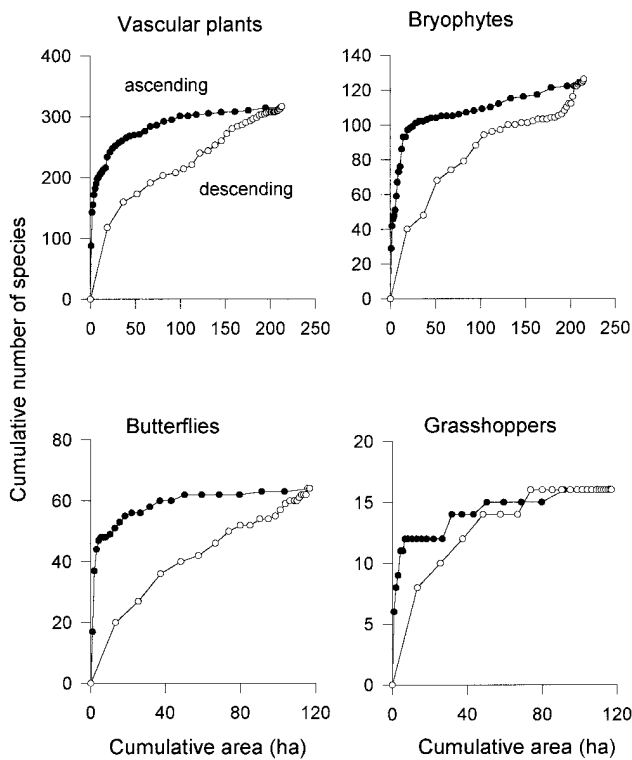


Fig. 2. Cumulative species-area relationships for four taxonomic groups ($n = 36$ for vascular plants and bryophytes, $n = 23$ for day-active butterflies and grasshoppers). Habitat islands are ranked along the x-axis in the order of ascending (filled symbols) or descending area (open symbols). Each step between two symbols on the curve can be viewed as the addition of one habitat island to an archipelago of islands.

also live in the intervening habitat matrix (generalists) or because they could easily disperse across it (mobile species). This may explain why we found the lowest z-value for bryophytes, only a few of which could be considered specialists for calcareous fens.

(4) We (as well as previous authors) could also have underestimated the slope because we considered only species richness as random variable with error and treated habitat area as fixed variable. If in fact habitat area also had associated error variation (defining the perimeter of a habitat island is not an easy task), then the z-values are always systematically underestimated in ordinary least-squares regression analysis (LaBarbera 1989, Schmid et al. 1994). This problem becomes more severe if the statistical correlation between the two variables is weak as in our study for the bryophytes and grasshoppers, which in turn may be due to other, non-confounding factors increasing variation in the data (in our study the classification factors management and altitude; see Peintinger 1999, Wettstein & Schmid 1999, Bergamini et al. 2001b). Furthermore, the errors-in-variables problem is also larger if the range of values is

small, relative to potential errors. In our study, habitat area ranged from 0.9–18.5 ha which is smaller than in other studies (see comprehensive lists in Conner & McCoy 1979 and Lomolino & Weiser 2001).

SLOSS question

In contrast to the suggestion of Wilson & Willis (1975) and Diamond & May (1976), the cumulative species-area curves for all four taxonomic groups showed that a collection of small habitat islands contained more species than one of a few large islands with the same total habitat area. This indicates that species overlap among habitat islands was rather low. Our findings are consistent with the results reviewed by Quinn & Harrison (1988) and papers published later (Virolainen et al. 1998, Tschardt et al. 2002). It confirms empirically the argument that the theory of island biogeography is neutral with respect to the SLOSS debate (Simberloff & Abele 1976) since SLOSS indices were larger than 1 despite the fact that the species-area relationships were positive.

Species compositions of three of the four investigated taxonomic groups were different between mown and grazed habitat islands (Peintinger 1999, Wettstein & Schmid 1999, Bergamini et al. 2001b). Thus, species overlap could have been small because of the study design. However, separate analyses of cumulative species-area relationships for mown and grazed habitat islands showed that the SLOSS indices were even larger in the separate than in the analyses of the complete data set (vascular plants: 1.30 in mown vs. 1.35 in grazed fens, bryophytes: 1.39 vs. 1.51, butterflies: 1.78 vs. 1.54, and grasshoppers: 1.22 vs. 1.53).

In real landscapes, small fragments are often not simply a random subset of the larger ones. Abiotic factors of the habitat islands differ on the geographic scale. Our habitat islands were dispersed over an area of 3500 km² that covered four different physiographic units (*sensu* Gutersohn 1978). As a result, several small habitat islands capture more habitat subtypes and perhaps much greater environmental heterogeneity than one large fragment (Tschardt et al. 2002). Moreover, regional species pools may differ in the studied regions because our study sites vary in topography, geology, and glaciation history. Consequently, the local species composition may also be different even if abiotic conditions do not vary among the habitat islands (Pärtel et al. 1996). Taken together, this may explain the high total number of species in a set of small fragments at the landscape level.

Nestedness

Using the formerly applied metric and test statistics of Patterson & Atmar (1986) and Wright & Reeves

(1992), nestedness was found in the majority of the examined real or habitat islands (Boecklen 1997, Wright et al. 1998). Our results, based on the C-metric (Wright & Reeves 1992), support the idea that nestedness seems to be a general pattern of real and habitat islands. Furthermore, the comparison with data compiled by Boecklen (1997) shows that our C-values of the four taxonomic groups were intermediate in the range (Fig. 3). This comparison also demonstrates, that species-rich taxonomic groups – bryophytes and vascular plants in our study – have been poorly studied.

In contrast, the analysis of nestedness using the N_a -statistic (Brualdi & Sanderson 1999) leads to a different result. None of the four taxonomic groups showed significant patterns. Evidently, the test statistic by Brualdi & Sanderson (1999) is more conservative than the C-metric. An important difference between the two methodical approaches is the construction of null matrices, namely the question whether species incidences should remain constant or not. Sanderson et al. (1998) and Brualdi & Sanderson (1999) argue that violation of column sums (incidence totals of species) does not sufficiently constrain the sample space of randomly generated null matrices. Therefore, the probability of type-I statistical error increases (see also Gotelli 2000). However, Gotelli & Entsminger (2001) have recently demonstrated that the recursive backtracking method of Sanderson et al. (1998) does not generate matrices equiprobably. Furthermore, they argue that an algorithm that maintains observed row and column sums is not the only valid way to generate null models.

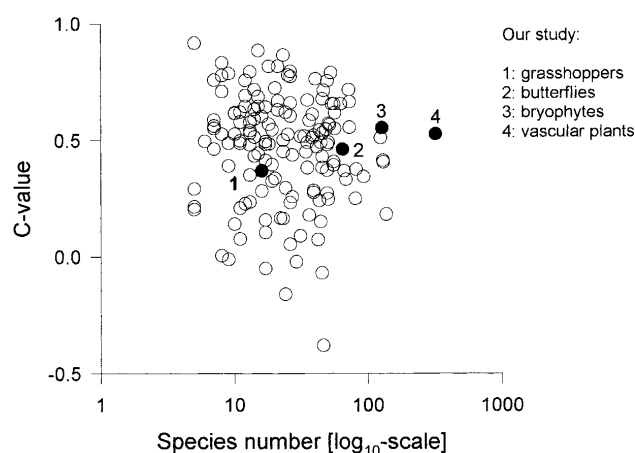


Fig. 3. The relationship between nestedness (C-values of Wright & Reeves 1992) and total species number (\log_{10} -scale) of 148 ecological communities compiled by Boecklen (1997: open symbols) in comparison to C-values for vascular plants, bryophytes, day-active butterflies, and grasshoppers in our study (filled symbols).

This shows that the debate about the correct construction of null models has been going on for more than two decades, but no method has yet been generally accepted.

In conclusions, the same matrix may yield random or significant patterns, depending on which metric and null model is used (Wright et al. 1998, Gotelli 2000). Consequently, nestedness as a tool for conservation management should not be implemented uncritically.

The analysis of nestedness is also proposed as a tool to examine the SLOSS-question (Wright & Reeves 1992, Worthen 1996, Ganzhorn & Eisenbeiß 2001). However, since matrices for nestedness analyses are ranked by species richness of islands (and incidence of species) and not by habitat area, nestedness analyses can only be used to solve the SLOSS question if there are strong species-area relationships. Connor & McCoy (1979) have shown, though, that this is rarely the case.

Diversity patterns of the four taxonomic groups

Species richness was not or only weakly correlated among the four taxonomic groups. Only for vascular plants and butterflies did we find a significant positive correlation. Besides the effect of area per se, this result could be explained by a more variable diet supply for either caterpillars or adult butterflies in habitat islands with more vascular plant species. Thus, there is no 'hot spot' in the sense that species richness of all groups is high within the same habitat islands (Reid 1998). Consequently, no single taxonomic group can be used as indicator group for overall species diversity (Prendergast & Eversham 1997).

However, the comparison between species richness of plants and of insects was unbalanced because insects may just be visitors that are not strongly associated to the studied habitat islands (in contrast to the sessile plants).

Implications for conservation

In summary, species-area relationships showed that species richness within habitat islands increased with area, but overlap among them was low enough that even small habitat islands contributed markedly to the overall species richness at the level of the entire archipelago of islands. However, for rare habitat specialists, large habitat islands may be necessary to maintain minimum viable population sizes and to minimise extinction risk (Soulé 1987). Therefore, a mosaic of several wetland islands, including small and large ones, is necessary to maintain species diversity at the landscape level.

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