Biogeography of vascular plants on habitat islands, peninsulas and mainlands in an east-central Swedish agricultural landscape

Martin Köchy* and Håkan Rydin

Department of Ecological Botany, Uppsala University, Villavägen 14, S - 752 36 Uppsala,
Sweden

*Present address: Department of Biology, University of Regina, Regina SK S4S OA2, Canada

Abstract

The increase of island species richness with area can be explained by an increase in habitat diversity or by an equilibrium of species immigration and extinction. We examined vascular plant species richness in 39 sites (24 habitat islands, 7 'habitat peninsulas' and 8 comparable 'mainland' sites). We sampled at three scales: whole sites, meadows within sites and quadrats (4 m x 4 m) within meadows. All sites ($10 - 10^4 \text{ m}^2$) contained natural vegetation within arable fields in east-central Sweden. There was a strong correlation between species richness and area for whole sites and for meadows. There was no correlation, however, between species richness in quadrats and site area. The difference between site and meadow results on one side and quadrat results on the other suggests that species richness increases with whole site area primarily because large sites are more diverse than smaller ones. Species-area relationships did not differ between islands, peninsula and mainland sites. Thus, patterns of species richness on our sites were more consistent with habitat diversity than an immigration-extinction equilibrium.

Introduction

Plants can modify their environment by positive feedback loops (Hobbie 1992). Therefore, it is important for the study of ecosystem function to determine to what extent ecosystems are controlled by habitat heterogeneity. A classic dilemma in island biogeography is whether it is possible to separate and test the different explanations for the positive species-area relationship. The increase of species richness with island size can be explained by several models. The random sampling theory (Arrhenius 1920, 1921) shows that a positive species-area relationship arises when individuals from a species pool are distributed at random over a set of islands[footnote]. The equilibrium theory states that the number of species on an island is determined by a dynamic equilibrium between immigrating species and species becoming extinct on the island (MacArthur & Wilson 1967). The habitat diversity theory argues that the number of species is a function of the number of available habitats on the island (Williams 1943).

The competing models were tested by many researchers by comparing their predictions to real systems or by statistically separating the effects of habitat diversity and area. The tests were not always critical of the tested theory and sometimes the tests even were inadequate (see Simberloff 1976, Connor and McCoy 1979, Gilbert 1980, Coleman et al. 1982, McGuinness 1984). Westman (1983) introduced an approach to separate the equilibrium theory from the habitat diversity theory as explanations for positive species-area relationships. Consider samples of fixed size (i.e., quadrats) on islands or mainland sites of varying area. The quadrats are laid out in similar habitats to exclude confounding with habitat diversity. Since quadrats have the same area and are put in the same habitat one would expect the same number of species per quadrat if species were distributed at random in the habitat.

In contrast, according to the equilibrium theory (MacArthur & Wilson 1967) there will be a positive influence of island area on the number of species per quadrat: as species become extinct in the quadrat the chance of recolonisation increases with island size because the extinction rate on the whole island is assumed to decrease with island size. This part of the equilibrium theory is closely related to the spatial mass effect (e.g., Shmida & Wilson 1985). A spatial mass effect is created by propagules of species dispersing into a habitat that does not otherwise support a growing population of this species and can thus be regarded as one of the mechanisms behind the equilibrium theory (MacArthur & Wilson 1967: 16).

Equilibrium theory further predicts that species richness increases faster with total area on islands than on mainland sites because the number of possible source species and source habitats outside (MacArthur & Wilson 1967) increases in the order islands – peninsulas – mainland. As, under the assumption of the equilibrium theory, the number of species per quadrat depends on the number of species of the whole site, the number of species per quadrat should also increase in the order islands – peninsulas – mainland.

Quadrat sampling has been used for vascular plants on true islands by Westman (1983) and Kelly et al. (1989). Both found species-area correlations to be weak and rejected the equilibrium theory. Tangney et al. (1990), however, studying bryophytes in the same sites as Kelly et al. (1989) found a positive correlation, compatible with the theory. Hill et al. (1994) found that some, but not all, of the species-area relationship of forests in Ghana could be attributed to random sampling. These examples suggest that applicable theories vary with taxa (cf. Case & Cody 1987) and whether sites are true or habitat islands. Species richness is also correlated with latitude (Currie 1991) and different theories accounting for species-area relationships at lower latitudes may not be applicable at higher latitudes.

The aim of this paper is to test predictions from the equilibrium and mass effect theory by applying the quadrat sampling method on a set of habitat islands at boreal latitudes.

Material and methods

We used the quadrat sampling method on a group of habitat islands within cultivated fields. Field islands (Swedish: åkerholmar) are excluded from tillage because of rocks (0.5 m to >5 m in diameter). Field islands and field 'peninsulas' typically consist of forb-rich grasslands and groups of trees ranging from small clusters to forests. Field island size ranges from <1 m^2 to >1 ha and the distinction between a large field island and a 'mainland' forest is arbitrary.

The study was conducted within a mostly flat area of 1.5 km^2 in Dalby parish (59°46'36"N, 17°33'48"E; 20-30 m a.s.l.), 12 km SSW of Uppsala, Sweden (Fig. 1) in the boreo-nemoral zone (Sjörs 1963). The regional vegetation is a mosaic of arable land, meadows, pastures and semi-natural spruce (Picea abies) and pine (Pinus sylvestris) forests that in historic times have been used for timber. Detailed maps from 1743, 1791, 1860-80, 1913, 1953 and 1980 show that the changes in landscape and in agricultural use during the last 250 years were small, and that the field islands, pensinsulas and mainland sites have existed in nearly the same shape as today (Köchy 1991). Today, none of the field islands are hayed or grazed by domestic animals. We found no indication of recent clear-cutting or systematic logging in the forest sites but individual trees have apparently been harvested at some sites within the last decade. We examined the species richness of 39 sites with natural vegetation: 24 field islands, 7 field peninsulas and 8 comparable mainland sites within surrounding spruce forest. Island area ranged from 10 m^2 to 7192 m^2, peninsulas from 88 m^2 to 12 291 m^2, and mainland sites were between 96 m^2 and 7002 m^2. One island divided by a narrow trench in 1985 was treated as one site. Mainland sites were selected to include a grassy area under an open tree canopy that visually resembled a meadow on an island. The decision of how much of the forest to include in the site was guided by existing landscape features, e.g., fence lines, ground edges or elevations.

We distinguished three habitats on our sites: margin, meadow and forest. Margin was defined as a 1 m wide zone inside the island or peninsula border. Its vegetation consisted mainly of perennial grasses (Tab. 1). Meadow was defined for the purposes of this paper as a grass-dominated area covered by more than 90% vascular plants in the field layer. The tree canopy cover was generally low, but reached almost 90% in a few instances. We applied the percentages to soil-covered areas only but included areas of bare rock into the habitat because some specialist species usually occurred in the cracks. Meadow vegetation was dominated by the grasses <u>Deschampsia flexuosa</u> and <u>Agrostis capillaris</u> and also contained many forbs (Tab. 1). Larger meadows included some shrubs and trees (mainly <u>Juniperus communis</u> and <u>Pinus sylvestris</u>). Forests were defined for the purposes of this paper as having more than 90% tree canopy cover. Most common tree species in our sites were <u>Pinus sylvestris</u> and <u>Quercus robur</u> (Tab. 1).

We chose this particular group of field islands because a large number of undisturbed field islands and peninsulas were concentrated in a small area and constituted a large range of size. We therefore assume that differences in soil type and local climate have no significant effect on the variation of species richness among sites.

We estimated cover of all vascular plant species separately for margin, meadow and forest, and for the whole site during May/June 1990 and July/August 1990. It took one person 10 min on the smallest (10 m^2) and 4-5 h on the largest site ($12\,291 \text{ m}^2$) to search for all species. Species cover was estimated using the Braun-Blanquet scale (Mueller-Dombois & Ellenberg 1974) and converted to percentages for statistical analysis. On the largest sites we found two to four species in the quadrats that we had overlooked in the whole-site search, implying that the total number of species may be underestimated by about 5%. Site areas were determined from maps and field measurements.

Species richness and quadrats

We established three quadrats (4 m x 4 m) in the meadow habitat to describe the change of species richness per quadrat with site area. The smallest sites could accommodate only one or two quadrats. In total 37 meadows were large enough to host at least one quadrat. We used a systematic procedure to place two of the three quadrats. Their centre point was determined by the following rules: 1. Start from the southernmost corner of the meadow (start from another cardinal direction clockwise if the shape of the habitat so requires). 2. Measure the distance from that point to the closest habitat border due North. 3. Place the first quadrat at half this distance with one diagonal running N-S. The second quadrat was placed by the same rules but starting from the opposite habitat side. When there was only one way to fit the quadrats into the habitat area on small islands the rules were not applied. The third quadrat was placed subjectively to cover parts of the meadow that seemed to differ floristically from the first two. All quadrats were searched for vascular plant species. We calculated the mean number of species in systematic and subjective quadrats for each site and compared the means by a paired t-test to decide if we could lump both categories. There were on average two more species in subjectively than in systematically laid quadrats. The difference was close to significance both when we compared all sites (SD = 4, t = 1.90; n = 26; P = 0.07) or only islands (SD = 3; t = 1.6; n = 14; P = 0.13). Therefore, we decided to analyse quadrat data in two ways: both systematic and subjective quadrats lumped and subjective quadrats excluded.

For the comparisons, quadrats must be restricted to one habitat that is fairly homogeneous within and among sites; otherwise the quadrats might also measure habitat heterogeneity. To ensure that meadows were homogeneous we sorted the meadows by area, calculated the similarity between successive pairs and excluded meadows with a similarity of <30% to a larger site. We used the Ellenberg-Jaccard index, $IS_E = 0.5M_c / (M_a+M_b+0.5M_c) \cdot 100\%$ (Mueller-Dombois & Ellenberg 1974) to calculate similarity, where M_c is the sum of percent

cover of the species common to meadows A and B, and M_a and M_b are the sums of percent

cover of species unique to meadow A and B, respectively. After the exclusion we retained 15

islands (mean IS_E = 54%), 7 peninsulas (mean IS_E = 42%), and 7 mainland sites (mean IS_E =

43%) for all statistical analyses. With one exception the meadow area of all excluded sites was

<60 m^2. We obtained the same set of sites whether we compared similarity among all sites or

among island, peninsula and mainland sites separately.

We regressed number of species per quadrat on the $\log_{10}$ of whole site area and compared

the slopes between island, peninsula and mainland sites by analysis of covariance (ANCOVA,

Zar 1984).

Species richness and area

Several mathematical models have been used to describe the relationship between number of

species and area. To determine which of the two-parameter models would fit our data best we

compared the goodness of fit (R^2) of the 'power model', $S = cA^z$ (Arrhenius 1920, Preston

1962, MacArthur & Wilson 1967), the 'logarithmic model', $S = c + z\log A$ (Gleason 1922), and

the 'transformed power model', $\log S = c + z\log A$ (Preston 1962, MacArthur & Wilson 1967)

which behaves different in statistical analyses than the untransformed model (Rydin &

Borgegård 1988). In the equations above, S is number of species, A is area, and c and z are

fitted parameters. We used the decadic logarithm ($\log_{10}$) where applicable. All models were fit

by minimising residual sum of squares. We compared the models for whole islands (i.e.,

margin, meadow and forest lumped) because meadow and total area were highly correlated (r =

0.95, Tab. 2) and meadow and forest species composition within islands was 50% (IS_E)

similar. We used the model that best explained the species-area relationship for islands also for

calculating the species-area regressions for the peninsula and mainland sites. We compared the

regression slopes by ANCOVA.

The range of area studied is known to affect the slope of the species-area curve (Williams 1943, Martin 1981). After excluding dissimilar sites the area range of island, peninsula and mainland sites overlapped for the greatest part and we did not have to exclude any other sites.

Habitat descriptors

We visually estimated the portion of island area consisting of bare rock and the portion of meadow area covered by trees. We assumed that these variables were important habitat descriptors because tree cover reduces available light and rocks limit the rooting zone. Rocks were usually evenly distributed across the islands so that the rock cover of the whole island also represents meadow rock cover. We determined the isolation of islands by measuring their distance to the closest larger island or the mainland on a map. We also calculated a weighted isolation index (I_i) for each island i based on the distance (d_{ij}) to all islands j (or the mainland) within a 50 m radius weighted by their area (A_j): $I_i = \Sigma \, e^{-d_{ij}} A_j$. This index produced weaker correlations with species richness than the former approach and we do not report results for the weighted isolation index.

Results

Species richness per quadrat area

Mean species richness in quadrats did not increase significantly with site area (Fig. 2). This result did not change when the data were analysed separately for island, peninsula and mainland sites, when meadow area was used instead of total area or when subjective quadrats were included. As species richness in quadrats did not increase with area we compared mean number of species per quadrat between island, peninsula and mainland sites. There was no significant difference in species richness among degrees of 'islandness' (ANOVA, $F_{2,28} =$

0.03; P = 0.97). This result was consistent whether we lumped peninsula and mainland sites or excluded subjective quadrats. Thus, quadrats contained on average 17±4 species (mean ± SD).

Species richness per site and per habitat

Number of species increased with total island, peninsula and mainland site area. Comparison of R^2 and residuals showed that the logarithmic model S = -42.47 + 42.62 logA ($R^2 = 0.80$; n = 15; Fig. 3) was the most appropriate for regression of number of species on whole island area (power model: $R^2 = 0.78$, transformed power model: $R^2 = 0.77$). The fit was less good when island, peninsula and mainland sites were analysed as one set (S = -18.61 + 34.17 logA; $R^2 = 0.75$; n = 29; Fig. 3). For meadows alone, the best model was the power model S = 15.76 $A^{0.216}$ ($R^2 = 0.70$) for islands and S = 16.26 $A^{0.211}$ ($R^2 = 0.64$) for islands, peninsulas and mainland sites combined.

The slope of the logarithmic model decreased in the order islands (z = 42.62) – peninsulas (28.79) – mainland (21.90), but ANCOVA was not significant ($F_{2,25} = 2.94$; P = 0.07). When peninsulas and mainland sites were lumped (z = 26.99) slopes were significantly different ($F_{1,25} = 4.63$, P = 0.04). When the non-linear power model was used for regression of species number in meadows and meadow area (islands: z = 0.216, peninsulas: z = 0.153, mainland: z = 0.242) the 95%-confidence intervals of the slopes overlapped (SAS Institute Inc. 1989) , suggesting no significant difference among exponents. Confidence intervals also overlapped when peninsula and mainland sites were lumped (z = 0.197).

Species richness and habitat descriptors

Habitat descriptors did not predict species richness as well as area. As tree and stone cover were closely correlated we devised an integrated index canopy as (1 – stone cover + tree cover)/2 for further evaluation. It explained 69% of the variation of island species richness.

The improvement in adjusted R^2 when adding habitat descriptors or distance to area in a multiple regression was marginal.

Among the independent variables there were positive correlations between total area, habitat areas and tree cover. Area was closely correlated with stone cover (Tab. 2). Variables correlated with total area were similarly correlated with species richness.

Discussion

Number of vascular plant species in meadow quadrats was independent of island size (Fig. 2) and even independent of 'islandness' and isolation (Tab. 2) in spite of a strong species-area relationship for the whole sites (Fig. 3). This is contrary to predictions from the equilibrium theory but conforms to Kelly's et al. (1989) and Westman's (1983) findings. Kelly et al. (1989) found negative relationships between species richness in quadrats and log-island area for all but one habitat subgroup in their study on forested islands in New Zealand. Westman (1983) also observed a negative correlation between species richness in quadrats and log-island size (r= -0.53) while overall species richness significantly increased with island area.

A few studies have yielded a positive relation between species number per quadrat and island size. On islands off Shetland, Kohn & Walsh (1994) reported an $R^2 = 0.07$ (logarithmic model) for the relation, which increased to $R^2 = 0.32$ when sampling was restricted to one habitat type. Kelly et al. (1989) found a positive relation for one out of five habitat subgroups ($R^2 = 0.42$, logarithmic model). Tangney et al. (1990) in their study of bryophyte species richness using the same sites as Kelly et al. (1989) also found positive correlations ($0.28 < R^2 < 0.63$, logarithmic model), a result compatible with the equilibrium theory. The authors, however, claim that their results (and those of Kelly et al. 1989) could also be explained by what they call the small island habitat hypothesis: the quality of a habitat differs between small

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and large island and is probably often more favourable on larger islands. The quadrat sampling method will not distinguish between the equilibrium theory and the small island habitat hypothesis.

In the field islands, a small island habitat effect could be caused by the fact that soil cover is often thinner and stone cover is higher on small islands than on large ones. Such a relation was described by Houle (1990) who found a correlation between soil depth and area in granite outcrops and that soil depth was the best predictor of species richness. Our data also suggest threshold effects: Meadows between 1 and 16 m^2 contained 7 to 10 species without any obvious area effect. Forests occurred only on islands larger than 125 m^2.

The species-area relationship for the field islands was strong (Fig. 3) and distance did not show any significant effect on species richness (Tab. 2) except through a correlation with area. The lack of a significant isolation effect is not unique to habitat islands; most botanical studies of real islands show no or very weak isolation effects on species richness (Nilsson & Nilsson 1978, Westman 1983, Buckley 1985, Nilsson et al. 1988, Rydin & Borgegård 1988, Hogg et al. 1989, Kelly et al. 1989, Tangney et al. 1990, Heatwole 1991, Soulé et al. 1992). In fact, the few cases where there seem to be distance effects come from studies of habitat islands (Nip-van der Voort et al. 1979, Dzwonko & Loster 1988, Houle 1990). Rydin & Borgegård (1988) found that peninsulas had more species than islands (in a lake) of comparable size, which did not seem to be the case with the field islands. **Most of the 208 species found on our island sites can be distributed by wind (65%) or by animals (epizoochorous: 20%, endozoochorous: 39%, by ants: 21%). Fewer species can be distributed by water (15%) or use their own means (16%) (Rothmaler 1982).** Most wind-dispersed seeds travel distances of 4-100 m, and Pinus and Betula seeds up to 2 km. Mice and ants disperse seeds within a 100 m radius, larger animals up to several km. Plants dispersing by runners or special mechanics cover distances of 0.2-15 m (Müller-Schneider 1977). Consequently, according to

these literature data most island sites were within the potential dispersal range of most encountered species.

We did not find strong evidence for the predictions from the equilibrium theory. The effect of islandness on species-area slopes was only significant when peninsulas and mainland were lumped and the logarithmic model was used. A lack of difference between island and mainland slopes of species-area curves, however, is not uncommon, and the scatter of the data points is usually great (Gilbert 1980). This may be taken as a general indication that a mass effect is usually of little importance. The effect of distance on the magnitude of a mass effect was tested by Hatton & Carpenter (1986). They found that on a 2-year old reclaimed mine site species richness of parallel transects at varying distance from the species pool decreased with distance. We argue that in this case colonisation of 'permanent' species was not yet finished (Rydin & Borgegård 1988, Villa et al. 1992) and that therefore Hatton & Carpenter's results cannot be compared with results from sites with a longer colonisation history as in the aforementioned studies.

Westman (1983) concluded that increasing species richness with island area was caused by increasing habitat diversity on larger islands rather than by reduced extinction pressure as assumed by the equilibrium theory. Using path analysis, Kohn & Walsh (1994) found that more than half of the area effect was through an indirect influence of area on habitat diversity. This may also be true for the field islands as the canopy cover was significantly correlated with area and predicted species number well (Tab. 2). Thus, species richness may be best explained by the habitat diversity hypothesis, although random sampling cannot be ruled out. Less stone cover was usually encountered when the rocks were smaller, probably creating suitable sites for plants with a deeper root system and less drought tolerance (Houle 1990). Also, the size of the forest part of the islands increased with island size and contributed to the species-area curve. More tree cover means more habitats for shade-tolerant plants, a trend that, however,

may be reversed at high degrees of cover (Rejmánek & Rosén 1992). An influence of tree cover was also found by Dzwonko & Loster (1988) for woodlots in the Carpathians. Numerous other studies found support for the habitat diversity model when it was compared to the equilibrium theory model (e.g., Buckley 1985, Dzwonko & Loster 1988), but this is not always the case (Simberloff 1976, McGuinness 1984, Nilsson et al. 1988, Rydin & Borgegård 1988).

Case & Cody (1987) stressed that different explanations are needed for different taxa and island systems, and that several complementary species-area models are required. The examples cited show clearly that there are difficulties with all attempts to separate the effect of area from that of habitat diversity or quality, and we argue that there will always be some correlations between area and habitat diversity in natural systems. Support for the 'area per se' hypothesis in studies where habitat diversity is uncorrelated with area (e.g., Nilsson et al. 1988) always raises suspicions about the observer's ability to define a habitat in terms that are relevant to the studied organisms. This problem also encounters the user of the quadrat sampling method. In our study the meadows seemed reasonably similar but the correlation between meadow area and tree cover exemplifies the problem, even though this variable was uncorrelated with species richness in quadrats.

The shadow thrown on the equilibrium theory's validity by application of the quadrat sampling method and the difficulties to separate the predictions made by different species-area theories demands more detailed studies of MacArthur and Wilson's (1967) assumptions about the relations between immigration and extinction rates, population size, island area and isolation. The difficulties in interpreting species-area relationships from quadrat sampling have recently been discussed by Rosenzweig (1995). We believe that the method may be a useful tool for testing predictions from the equilibrium theory and mass effect, but will not distinguish between random placement and habitat diversity as alternative explanations for species-area relationships.

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Footnote to page 3

[1]The correct form of Arrhenius' equations for the relation between species number and area is

$y^{\log(q)} = a^{\log(q)} \cdot (x/b)^{\log(o)}$, where x is the number of species in a patch of area y, b is the number of species on an area of one unit (a), q is the increase in species number as area increases with the factor o. It has been misprinted at least three times. In the original paper, a doctoral thesis (Arrhenius 1920), log(q) was omitted from the right-hand part of the equation. In the subsequent 'correction' in Journal of Ecology (Arrhenius 1921) the7 letters 'o' and 'q' were reproduced as the numbers '0' and '9'. Using the nowadays common symbols, McGuinness (1984) quoted the formula as $A^{\log 9} = C^{\log 9}(S/Z)^{\log 9}$.

Table 1. Mean species cover (%) for all sites. Only the 20 species with the highest average cover are listed. A listing of the abundance of all species is available on request from the authors.

Species	Average	Margin	Forest	Meadow
Agrostis capillaris	8	7	6	10
Deschampsia flexuosa	8	<1	12	11
Pinus sylvestris	6	<1	14	5
Dactylis glomerata	6	8	5	5
Quercus robur	6	1	14	4
Agropyron repens	5	10	1	5
Alopecurus pratensis	5	9	2	5
Juniperus communis	5	0	10	6
Populus tremula	5	3	10	4
Agrostis stolonifera	5	8	2	4
Phleum pratense	5	10	1	3
Sorbus aucuparia	5	1	9	5
Poa angustifolia	4	3	2	7
Poa compressa	4	6	2	5
Anthriscus sylvestris	4	4	2	5
Picea abies	4	1	10	1
Achillea millefolium	4	5	<1	5
Trifolium pratense	3	4	1	4
Rubus idaeus	3	2	3	5
Prunus spinosa	3	2	6	2

Table 2. Pearson correlation coefficients for variables associated with the habitat islands. Coefficients in the upper half of the matrix are based on the 15 islands used in regression analyses, and coefficients in the lower half are based on all islands (n = 24, except S_{quadr}: n = 21). S_{tot}, total species number on the island; S_{mead}, number of species in the meadow habitat; S_{quadr}, mean species number in the systematic quadrats; A_{tot}, total site area; A_{mead}, area of the meadow habitat; tree cover, percent of meadow habitat covered by trees; stone cover, percentage of rock and stone cover on the whole island; canopy = (1-stone cover + tree cover)/2; distance, distance to the nearest larger island or to the mainland.

	S_{tot}	S_{mead}	S_{quadr}	$\log(A_{tot})$	$\log(A_{mead})$	tree cover	stone cover	canopy	distance
S_{tot}	1	0.94***	0.11	0.90***	0.85***	0.85***	-0.54*	0.83***	0.04
S_{mead}	0.97***	1	0.32	0.82***	0.84***	0.75***	-0.41	0.70**	0.21
S_{quadr}	0.31	0.44*	1	-0.10	-0.12	-0.17	0.34	-0.28	0.34
$\log(A_{tot})$	0.94***	0.9***	0.17	1	0.95***	0.81***	-0.46*	0.76***	0.16
$\log(A_{mead})$	0.92***	0.91***	0.15	0.97***	1	0.76***	-0.49*	0.75***	0.24
tree cover	0.68***	0.64***	0.06	0.65***	0.64***	1	-0.48*	0.90***	-0.10
stone cover	-0.70***	-0.65***	-0.08	-0.65***	-0.67***	-0.51**	1	-0.82***	0.26
canopy	0.80***	0.74***	0.08	0.75***	0.75***	0.88***	-0.86***	1	-0.19
distance	0.31	0.43*	0.37	0.42*	0.45*	0.07	-0.07	0.08	1

*, $P \le 0.05$; **, $P \le 0.01$; ***, $P \le 0.001$

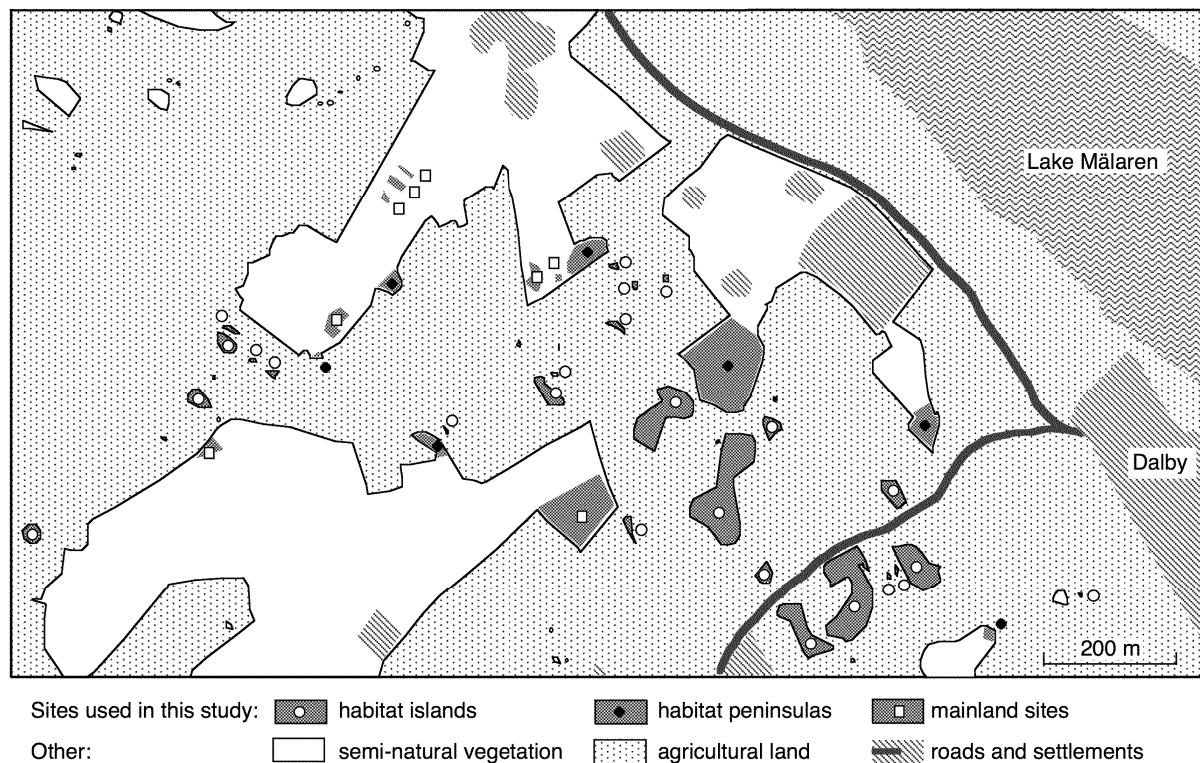Fig. 1. Location of the field island, peninsula and mainland sites.

Fig. 2. The relation between mean number of species per 16-m^2 quadrat and total site area.

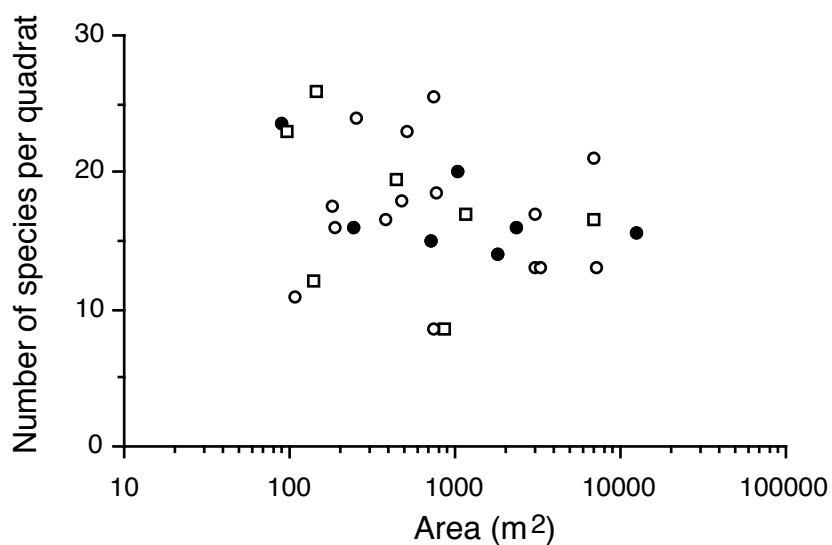O islands; ● peninsulas; □ mainland sites.

Fig. 3. The relation between species richness and site area for islands (O, solid line) and islands, peninsulas (●) and mainlands (□) combined (dashed line). The regression equations are S_{island} = -42.47 + 42.62logA (R^2 = 0.80, n = 15) and $S_{all\ sites}$ = - 18.61 + 34.17logA (R^2 = 0.75; n = 29).