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of vascular plants on field islands

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CONTENTS

i. Summary

In the district of Dalby, 12 km south of Uppsala, Sweden, I explored the species-area relationship for vascular plants on field islands (vegetation stands on mounds or small hills of moraine or rock forming 'islands' in arable land). The area of the field islands varied between 10 m^2 and 1 ha.

I applied an approach that was suggested by Kelly et al. (1989). The islands were divided into a margin, a forest, and a meadow habitat. I laid out 16 m^2 quadrats on the islands' meadows and counted the species. According to the equilibrium theory by MacArthur & Wilson (1963), the number of species in the quadrats should depend on the size of the field island because it is more probable on large islands that species that go extinct within the quadrat are replaced by other species living nearby but outside the quadrat. Two other hypotheses, the random placement and the habitat-diversity hypothesis infer that the number of species in quadrats is independent of island size.

The best two-parameter model for the number of species on the whole field island regressed on total island area was the logarithmic equation $S = g + k \cdot \lg(A)$. The z-value for the power equation model ($S = c \cdot A^z$) differed remarkably between the transformed ($\lg(S) = \lg(c) + z \cdot \lg(A)$) and the untransformed equation (0.35 and 0.27 respectively). This difference can however be explained mathematically. The mean of both z-values, 0.31, coincides with the value range ($0.20 < z < 0.35$) predicted by the equilibrium theory, but is also expected by other hypotheses. One prediction by the equilibrium theory, the difference in steepness between mainland and island curve slopes was met, but may be due to a different relation between habitat diversity and area.

No relationship between species number in quadrats and field island area was found. This indicates that extinction rate is not lower for small field islands.than for larger ones The distance to the mainland was not correlated to species richness. Thus two of the basic assumptions of the equilibrium theory are violated. This means that other mechanisms than those proposed by the equilibrium theory determine the number of species.

It was possible to show that number of habitats and three habitat variables (disturbance by human activity, tree cover on the meadow part, and portion of boulder) depend on area: Small field islands consist of a single boulder with a thin soil cover, therefore the number of species is small. Big field islands are found where the amount of rock keeps the farmer from ploughing, but the soil cover allows a richer vegetation and even trees or small woods may grow on it.

ii. Abbreviations

A	area
S	number of species
mar	margin, i.e. the one metre broad border stripe of a field island
mea	meadow, i.e. the mainly grassy, open part of a field island
for	forest, i.e. the wooded parts of a field island
cen	central part (margin plus meadow)
tot	total

| g, k | intercept and slope in the logarithmic equation |
| c, z | intercept and slope, respectively prefactor and exponent in the (transformed) power equation |

DIST	distance
QU_ALL	the mean number of species in all quadrats of one site
QU_SYST	number of species in a systematically laid quadrat
QU_SUBJ	number of species in a subjectively laid quadrat

| SE | standard error |

| lg(…) | the base 10 logarithm |

iii. Nomenclature of Plant Names

Plant nomenclature follows W. Rothmaler (1988, resp. 1982), Exkursionsflora für die Gebiete der DDR und BRD, vol. 2, Gefäßpflanzen, and vol. 4, Kritischer Band, Berlin: Volk und Wissen.

1. INTRODUCTION

The Relationship Between Species Number and Area on Islands

The relation between the number of species of one taxon and the size of the area (e.g. an island or a quadrat) they were sampled from, is one of the old favourites of ecologists, because "islands come closest to constituting discrete independent ecosystems or natural laboratories" (Slud, 1976, quoted in Gilbert, 1980). The mechanisms that demonstrably control species number on islands are also important mechanisms for community structure besides trophic interaction and space competition (Gilbert, 1980), since the environment of most communities will differ in some way from the surroundings and therefore represent a kind of island. The understanding of how species number is controlled on isolated islands will also help to improve our knowledge about how selection works and ameliorate evolution theories. The results may also serve for planning the size and establishing of nature reserves.

1.1. The Models

1.1.1. Power Model, Logarithmic Model, and Random Placement

Alph[onse] de Candolle's *Géographie botanique raisonnée* from 1855 is usually the earliest work cited by biogeographers. In fact, he was not the first to discuss species richness on islands and he disagreed with von Buch (1819, 1825) that islands had fewer species because they were islands. Olof Arrhenius stated in 1921 that generally the number of species is diminished on small islands compared to the mainland, but approaches the number of species on the mainland when the islands become large enough. For this relation he had earlier found (1920) the equation[*] $y^{\log(q)}=a^{\log(q)}\cdot(x/b)^{\log(o)}$ (where y is area, a is one unit area, x is the number of species on y, b is the number of species on a, and q is the increase in species number when area increases by the factor o), later simplified by him to $\frac{y}{y_1} = \left(\frac{x}{x_1}\right)^n$ (with two different large areas y and y_1 in the same habitat on which a number of x, respectively x_1 species live, n is a fitted constant), this makes $\frac{A_1}{A_n} = \left(\frac{S_1}{S_n}\right)^{\frac{1}{z}}$ in my notation and it is a special case of the power function $S = c\cdot A^z$ (McGuinness, 1984a). He wondered however, what the chances were to find a certain number of species on a certain area (of mainland) when they were distributed at random. Arrhenius calculated this to be $S_s = \sum_{i=1}^{S_t} 1 - \left(1-\frac{A_s}{A_t}\right)^{n_i}$ (He did not use the sum sign or these symbols: S for number of species, index s for sample, index t for total, n_i for number of individuals in the i-th species ['frequency']). This formula sums up for all species that exist in a given area (A_t) the probability to find a certain species in a sample (A_s) of that area (A_t) when the number of individuals (n_i) belonging to that species is known. The sum is the expected number of species in the sample. Arrhenius (1921)

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[*] This equation is misprinted in both the works by Arrhenius, that are cited here. It is also wrongly reproduced by McGuinness (1984). In the first statement of the equation in his difficult to access doctoral thesis one of the logarithms had been omitted. In the subsequent 'corrected' version, that Arrhenius published in the Journal of Ecology, the letters 'o' and 'q' were misprinted as the numbers '0' and '9'.

thought that the equation performs best when the species have a low degree of frequency. Coleman (1981) improved this hypothesis and called it the Random Placement Model respectively the Random Placement Theory. Instead of just assuming that the individuals of a species are randomly distributed over the sample area, his procedure is first to establish the species' abundance in terms of number and area. He then calculates the probability for how many of the observed species an island of a certain size could contain. With a little imagination one can envisage an animated island that randomly samples from the species pool and produces thus the so called 'sampling effect'. Gleason (1922) extrapolated uncautiously Arrhenius' equation to larger areas and by doing so overestimated species number. He proposed instead the logarithmic model $S = g + k \cdot \ln(A)$, refered to as 'exponential' by Connor & McCoy (1979), but he provided no mathematical derivation for this equation. This was done later by Fisher et al. (1943) and Williams (1964), assuming on the one hand the species' population size to be proportional to area and on the other hand a log-series relative abundance distribution. Preston (1962, see below), however derived the log-normal relative abundance distribution under similar assumptions and showed that Fisher's et al. and Williams' results might be due to sampling effects. McGuinness (1984a) consequently rejected the theoretical derivation of the logarithmic function. The following decades there was disagreement among the scientists which equation fitted the species-area-relation best and what biological meaning the parameters could have (see for example Connor & McCoy, 1979, Sugihara, 1981, Ekbohm & Rydin, 1990, Loehle, 1990).

1.1.2. Habitat-Diversity Hypothesis

In 1943 Williams examined published data about the number of species of flowering plants in areas ranging from 10 cm^2 to the size of the American continent (10^7 km^2). He divided the resulting curve into three regions which were fitted best by different equations. The exponential equation fitted best to observations on areas ranging from 10 cm^2 to 1 ha, and he agreed with Arrhenius (1921) that this could be explained by random placement. The next region from 1 ha to 10^7 km^2 was best fitted by the power function and Williams ascribed this to be the effect of the addition of more habitats. The last region consisted of only two points representing the addition of continents with different evolutionary history and was best fitted by the power equation, but with a steeper slope than in the preceding stage. The idea of explaining species diversity on isolates by habitat diversity was thereafter applied by many other researchers and was extended to other taxa and smaller areas. Until lately (Buckley 1979, cited in Buckley, 1982) there was however no theoretically derived equation accounting for the increase in habitat.

1.1.3. The Equilibrium Theory

The next step in the study of the species-area relation were the papers by Preston (1962) and MacArthur & Wilson (1963, 1967). Preston developed the power function curve assuming that the number of individuals belonging to the species in a complete community were log-normally distributed, i.e. there are more moderately rare species than moderately common ones. MacArthur & Wilson (1963, 1967) built on Preston's equations and enlarged upon the possible mechanisms for the reduction in species number in isolates and derived the power function model theoretically. They suggested that the number of species on an isolate should be the result of a dynamic equilibrium between

immigrations and extinctions[*]. Characteristic for this theory is that the mechanisms, i.e. immigration and extinction, are influenced by many factors that could appear in all situations. Thus, the degree of isolation, dispersal ability of possible immigrating species, size of species pool, population growth, habitat diversity and size of the place the species live in are integrated in the theory. In addition, the principle of these relations is not only valid for islands, but also for habitat islands and arbitrarily defined plots: habitat islands are surrounded by contrasting habitats (more or less hostile to the taxa studied) just like islands are surrounded by water.

MacArthur and Wilson suggested that first, when an island is colonized, immigration rate, expressed in number of arriving new species per unit time, is high due to the few species present on the island. At the same time extinction rate is low, since resources can be shared between few. With increasing number of species the probability that species go extinct (or leave the island) will rise, for example because of harder competition and immigration rate will decrease because most of the individuals arriving on the island will belong to species that are already present. The authors assume further that immigration rate decreases with distance from the mainland whereas extinction rate decreases with increasing area as a consequence of larger population size on larger islands. Consequently there will be a point where as many new species arrive as resident species go extinct. This they called the dynamic equilibrium. The relation between species number and area can with the help of Preston's mathematical models be expressed as $S = c \cdot A^z$. Preston (1962) predicted a value of 0.26 for z, a parameter which is often called the 'slope' according to the logarithmic transformation $\lg(S) = \lg(c) + z \cdot \lg(A)$ which is a linear relation. The parameter z reflects how much species number increases with area. Studies of real islands often produce a z-value within the range of 0.20 to 0.35 and for sample areas or habitat islands values for z may lie between 0.12 and 0.17. MacArthur & Wilson accepted these ranges as consistent with their theory.

The difference between mainland and island slope is produced by a higher number of 'transient' species on the mainland, i.e. species whose individuals live just outside the sample area and fill in gaps when individuals within the sample become extinct. Thus they raise the number of species in the sample. Especially mobile animals contribute in this way to the species turnover. This effect will be strongest for small sample areas on the mainland and diminishes when the sample area approaches the size of the mainland. As a consequence, species number will rise at a lower rate with area as it were the case for islands and therefore the z-value will be lower for samples than for islands. The lower z-values for mainland samples indicate thus that area is of less importance.

The larger the islands become, the more they will resemble mainland. At the same time immigration rate decreases because most species have already arrived on the island and thus the increase in species number per unit area will become lower and finally equal to slopes representative for mainland samples.

Higher z-values than predicted occur and can, according to the theory, be caused by high habitat diversity when the islands break up in subsets of widely differing habitats.

The parameter c is less determined and reflects mathematically the number of species that live in one unit of area. However, such interpretation is only meaningful when this point lies within the range of the measured data. Gould (1979) in contrast stresses that, when slopes attained for one system are very similar, then c expresses a size-dependent invariant that could give valuable information about the system.

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[*] This was in fact suggested prior to MacArthur and Wilson in a doctoral thesis in 1948 by E. G. Munroe, but was not paid attention to (Brown & Lomolino, 1989).

The slope value z is suitable for comparisons if some facts are observed (Connor & McCoy, 1979): z and lg(c) are biased by logarithmic transformation and have to be multiplied by a correction factor (Sprugel, 1983). The parameters are interdependent and one of both depends on the unit of measurement: the intercept in the transformed and the exponent in the untransformed model. Moreover, for comparison of z-values the range of area between the studies must overlap considerably and for intercept comparison the slopes have to be equal. Finally they cannot be compared directly unless the same statistical model was applied (linear regression on lg(A) or non-linear regression on S, least squares or reduced major axis method) (e.g. Connor & McCoy, 1979, and Rydin and Borgegård, 1988).

Comparing the slopes for different species-area curves has been criticised, for example by Connor & McCoy (1979), who showed that the constancy in z is rather a mathematical coincidence, and pointed out that only a deviation from the expected range, i.e. 0.20 - 0.35, might be biologically interesting.

In contrast to the other island hypothesis, the equilibrium theory is dynamic and explains species richness on two levels. First, by the immigration rates to the island and, second, by the conditions on the islands. The name '*area-per-se* hypothesis' is therefore unsatisfactory for the equilibrium theory.

1.1.4. Disturbance Hypothesis and Evolutionary Aspects

Other possible mechanisms were proposed to account for the species-area relationship, but have so far not become as prominent as the above mentioned. Rützler (1965), Sousa (1984, cited in McGuinness, 1984a), and McGuinness (1984b) suggested that in the system they studied (communities on intertidal boulders) disturbance events reduce the diversity of an area (because the spatial dimensions of the force in action are many times larger than the observed species' universe. The events were more drastic and more frequent on small islands and according to these authors they play a major role in the species-area relation.

Begon, Harper & Townsend (1988), Webb (1969, in Gilbert, 1980), Janzen (1969, 1973, both cited in Gilbert, 1980), and Gilbert (1980) stress the importance of evolution in the species-area relationship. Evolution was shown to be the cause for the numerous *Drosophila* species on Hawaii (Begon, Harper & Townsend, 1988), and recently introduced plants and animals that once were established free from parasites seem to support less parasitic species than in their places of origin (see e.g. Southwood et al., 1982 [cited in Begon, Harper, & Townsend,1988]). Evolution was also invoked to account for the difference in species number for two African lakes that were created in different geological times (Fryer & Iles, 1972 [cited in Begon, Harper & Townsend, 1988]).

Although it seems that all these theories exclude each other, they are in fact comple-mentary (Begon et al., 1988; McGuinness, 1984a; Nilsson et al., 1988, Connor & McCoy, 1979, pp 793 and 814). But it is a task to separate the different mechanisms and to prove their existence.

1.2. Testing the Models

All models predict under the simplest assumptions that large islands support more species than small islands and that on a non-evolutionary time-scale species number should be constant. The reducing effect of increasing isolation is acknowledged by all

theories, but only the equilibrium theory treats isolation extensively. Other predictions, not necessarily obvious, but characteristic for each theory, can be used to test them against each other.

The random placement hypothesis (Arrhenius, 1921; Coleman, 1981) has been called the null-hypothesis (indirectly Connor & McCoy, 1979, see Coleman et al., 1982), "and all hypotheses invoking biological processes to explain the species-area relationship should be considered alternatives" (Connor & McCoy, 1979). Colwell & Winkler (1984) disagree with this kind of null-hypothesis: "The null-hypothesis tested in any analysis of biogeographical data ... is not that empirical patterns do not differ from random ones, but that they do not differ from patterns generated by a particular model of the world." They admit readily, that it may be very difficult to construct a such one. If now the random placement theory is considered an appropriate null-hypothesis (e.g. by Simberloff, 1976; Connor & McCoy, 1979; Coleman et al., 1982; McGuinness, 1984b), it should be tested first, before other models are considered as explanation for the species number distribution. Testing Coleman's (1981) variant of the null-hypothesis obviously involves that the abundance for all species and the area occupied by the individuals belonging to each species must be investigated on all islands. Deviations of observed values from predicted values must then be correlated to area to account for clumping or overdispersal of individuals (Abele & Patton, 1976) before one can reject random placement. This approach is time consuming and therefore costly, and Simberloff (1976) suggests a different strategy that produces results that enable to distinguish patterns consistent with the random placement hypothesis from those of other theories. The procedure involves sampling successively smaller, randomly placed quadrats from several large islands of similar size and counting the number of species in each sample. The thus established species-area curve can then be compared with the actually found numbers on small islands and tested for differences.

A general habitat-diversity theory that describes a mechanism that produces the species-area curve and makes testable predictions seems never have been stated. So far the habitat-diversity hypothesis has been considered valid for a certain study when the regression on habitat diversity gave a better fit than other competing models (e.g. Watson, 1964, cited in MacArthur & Wilson, 1967; McGuinness, 1984a). Yet, and not only in MacArthur & Wilson's (1967) opinion, showing that habitat diversity explains most of the variation is no proof that the mechanisms that control species diversity as proposed by the equilibrium theory are not in action. On the other hand, habitat-diversity was considered unimportant for studied systems when area was the best predictor for species richness and habitat variables were not correlated to area (e.g. Nilsson et al., 1988). But one can always argue that it is impossible to know whether all relevant habitat variables had been included in such studies. In some studies (e.g. Abele &Patton, 1976) it was possible to show that the sampled areas did not differ in habitat heterogeneity, but in spite of this species richness was dependant on area.

The equilibrium theory has been tested by many researchers and in the most different ways, not always critically, and sometimes even erroneous (see Simberloff, 1976, Connor & McCoy, 1979, Gilbert, 1980, Coleman et al., 1982, McGuinness, 1984a). A straightforward approach is to determine immigration and extinction rates for equally isolated islands, and to show that species number is in equilibrium and depends on mainly these two factors. This approach has seldom been applied because in its perfection it would be necessary to follow species turnover at all times and at all places of the investigated area; and defining immigration and extinction in an operational way is not easy at all (MacArthur & Wilson, 1967, Coleman et al., 1982). Approaches that try to verify predictions about z, the 'slope' in the transformed power equation, either about the value itself or the value for z for islands compared to the value for sample plots of varying size on mainland, can merely produce statistical evidence, but they cannot falsify the

mechanism - a common wisdom in statistics (see e.g. Connor & McCoy, 1979, McGuinness, 1984a). Most deviations can be explained by the equilibrium theory invoking anomalies (see MacArthur & Wilson, 1967, for examples).

Few reports have so far considered the role of disturbance as an explanation for species richness on islands (McGuinness, 1984a). General theoretical grounds for isolated areas are poor, since most studies in this aspect were carried out in intertidal zones, where disturbance by waves was high. Similar to the habitat-diversity hypothesis, the disturbance hypothesis is invoked, when it explains most of the variation in a study of species-area relationship.

The evolutionary hypothesis can only be interesting as an explanation when there are more new species produced by evolution than species that immigrate in the same time. This would be indicated when introduced species play some role in the studied system or when endemic species occur in the investigated area. Extinct endemic species can nevertheless obscure this hint. And not unlike the 'ghost of competition past', past evolution can explain many contemporary conditions, but so far it cannot foretell species number in the future.

1.3. The Object of Study:
    Stands of Vegetation Surrounded by Arable Land ('Field Islands')

The investigated habitat islands are called 'åkerholmar' in Swedish (singular: åkerholme) and I suggest 'field islands' as the corresponding English expression. These field islands are insular parts within a field and excluded from agriculture. The reason for this is that rocks and boulders, remnants from the last (Vistula) ice age, or the tops of ground rock hidden just below the surface hamper the plough or make ploughing impossible. The size of the rocks and boulders varies from c. 0.5 m to >5 m in diameter. The vegetation on field islands is not uniform. Most common are herb rich patches of grass with some individual trees or meadow-like open parts and woods, depending on island size (Fig. 1). The field islands' size covers the whole range from <1 m^2 to >1 ha and the distinction between a large field island and a patch of forest is arbitrary (Fig. 2).

The field islands resemble real islands as far as isolation from the mainland is concerned. Most plant species on the field islands are perennials and the fields around the islands are tilled annually, which leaves only the few annuals as possible survivors.

Until this century's first decades the largest field islands may have been used as pastures or meadows and smaller ones as a place to deposit stones collected from the fields. As far as trees grew on the islands they were used as a resource for timber and firewood. Today none of the field islands is grazed or mown, but they are still used as a stone deposit and evidently as resource for firewood as I occasionally saw felled trees. Most larger field islands are the home for hares (*Lepus lepus*) and badgers (*Meles meles*) they provide a resting place for roe deer (*Capreolus capreolus*), and are the ant colonies' kingdom.

1.4. Aim of this Study

Field islands as such have so far been paid little attention to although they are a conspicuous part of a landscape formed by ground moraines. This study is to elucidate the species-area relationship for field islands.
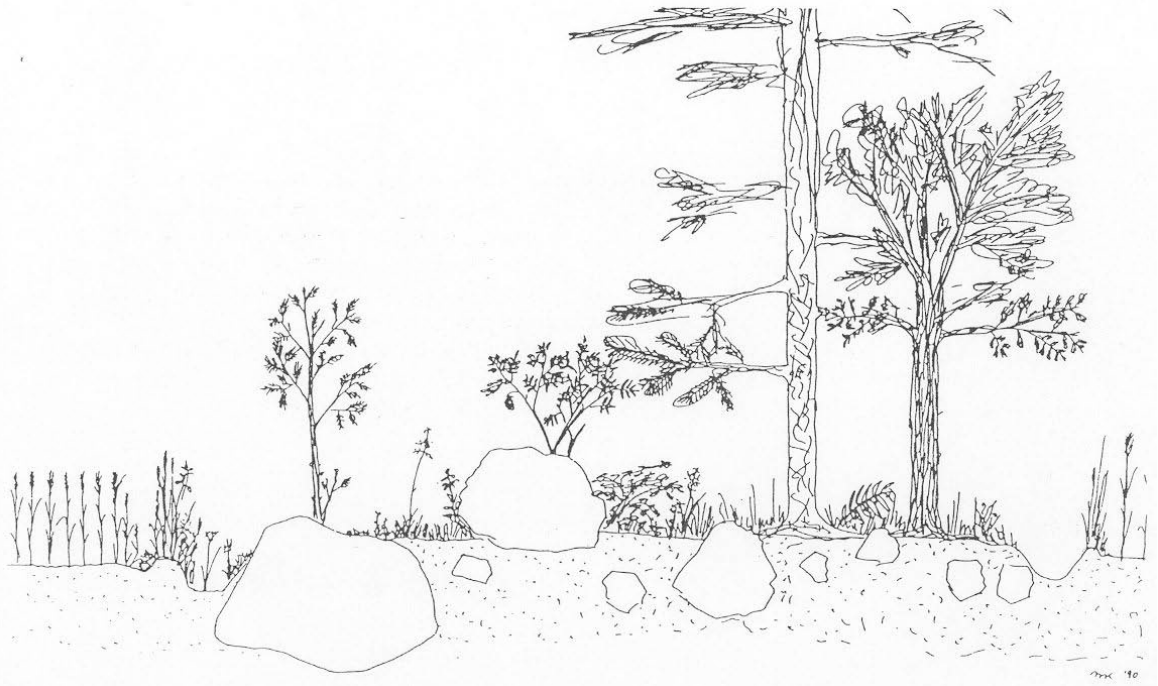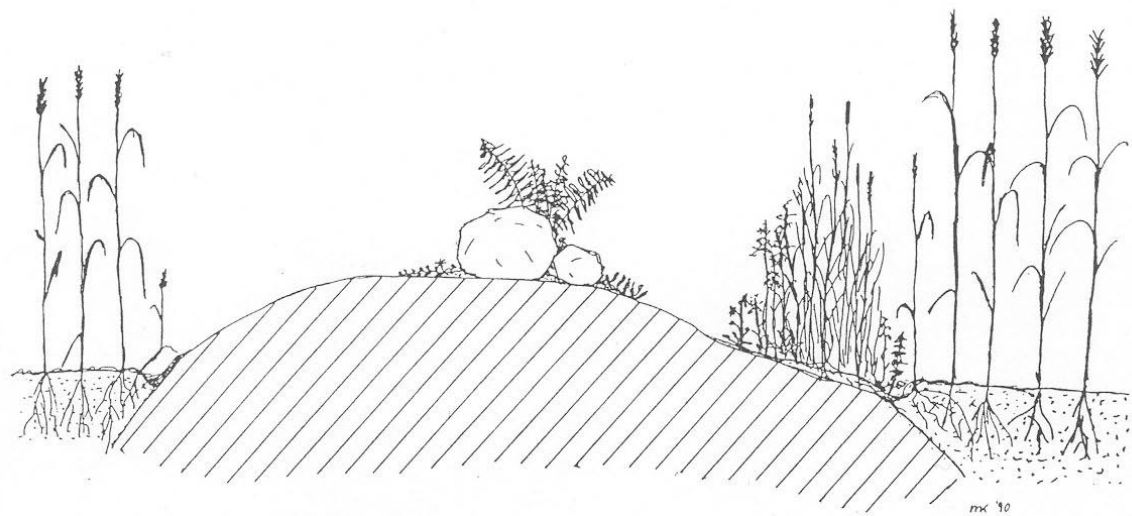
Fig. 1
Idealized cross sections of a small (top) and a large (bottom) field island.
Large field islands consist mainly of big rocks, with a deeper soil and therefore richer
vegetation than small field islands that often consist of only one boulder and no
accumulated soil. Observe that the drawings have different scales.

The most characteristic feature of islands is their isolation from the mainland and this gives rise to a number of questions, e.g. how many species are there on the field islands? –Most probably the number rises with area, yet this is not generally true: Connor & McCoy (1979) for example name 57 of 100 studies where the increase of number with area is nearly zero (z<0.01). And does isolation have an effect on the number of field isolation explain possible differences in species number? Other explanations cannot be excluded. Especially habitat diversity may be thought to determine species number. In this regard I want to highlight its dependence on habitat number and quality, approximately expressed through shadowing by trees, human disturbance, and portion of bare rock. Do the different habitats contribute equally to the total number of species? The area ratios between the habitat types or the degree of 'roundness' expressed by the ratio of perimeter to area might be measures for this.

I will not consider evolutionary explanations, since I did not find any endemic species on any of the investigated sites, and as all field islands are near to the mainland (the largest minimal distance was 120 m), I hardly expect gene flow (Kull, 1977) from and to the islands to be reduced compared to the gene flow within the mainland. The equilibrium theory as opposed to the hypotheses of habitat diversity and random placement predicts a geometric increase by 0.26 for oceanic islands and lower values for habitat islands and mainland sites. Whether this holds for the investigated sample of field islands has to be shown. A method recently proposed by Kelly et al. (1989) allows to test for the patterns in the species-area relationship produced by transient species, a feature of the equilibrium theory. This approach I would like to apply to the species-area relation of field islands.

1.5. The Study's Approach

The strategy I have followed had been suggested by Kelly et al. (1989). I will here render the method and their argumentation: MacArthur & Wilson (1963, p.382) quote Preston (1962, pp. 430 and 414): "[Island biotas] 'have far fewer [species] than do equal areas on a mainland.' To illustrate,' in a sample, such as the breeding birds of a hundred acres, we get many species represented by a single pair. Such species would be marked for extinction with one or two seasons' failure of their nests were it not for the fact that such local extirpation can be made good from outside the 'quadrat', which is not the case with the isolate.'" MacArthur & Wilson (1963) comment that "this point of view agrees with our own." Kelly et al. gather that the direct quotation of Preston makes clear that MacArthur and Wilson understood their own theory to predict that an area of a particular size on an island will have fewer species than an area of the same size on a mainland.

MacArthur & Wilson quote Preston like taking stones from a quarry -he certainly did not envisage a comparison between equally large samples on mainland and islands- and I doubt whether MacArthur & Wilson, when they arranged the quote-crumbs, intended an interpretation as Kelly et al. wants them to do. Although Kelly et al. misinterpreted the text passage, their conclusions follow likewise from the whole theory's model and this view can be found in MacArthur & Wilson's 1967 book (p. 16), even if the point becomes not as accentuated. "A small sample area [on the continent] carries more species than an island of the same size and similar environment ... It contains very small numbers of individuals ... belonging to species that are not well adapted to the sample area but are nonetheless represented because they persist in other places close at hand. In other words, there is a much higher immigration rate of transient species than is the case in the more isolated islands. (...) This advantage to non-isolated, continental sample areas diminishes, however, toward the upper end of the area scale. As the area is enlarged, it develops an ever more complete sample of the habitats on the continent as a whole." This shows that MacArthur and Wilson thought of a reduction in species number per unit area as island size diminishes.

Consider now samples of one size (quadrats) but mainlands or islands of varying area. The quadrats have to be laid out in similar habitats to exclude confounding with habitat diversity. Random placement within the quadrats can be excluded as well, because all quadrats are equally large. As the quadrats are not isolated, immigration rate must be the same for all quadrats. Likewise, extinction rates must be the same, because the quadrats have the same size. Therefore the quadrats should have the same number of 'resident' species. But a quadrat on a large island will contain more transient species than a quadrat on a small island and consequently the total number of species (transient plus 'resident' species) will be higher on the larger island. Thus according to the equilibrium theory there will still be an influence of island area on the number of species in the quadrats, whereas no such influence is predicted by the random placement or the habitat-diversity hypothesis.

The advantage of this approach is the possibility to test whether the premiss of the equilibrium theory -that extinction rate depends on area- is fulfilled. A negative outcome excludes this theory as an explanation for the species-area relationship without one having to take the trouble to monitor all immigrating and disappearing species.

2. MATERIAL AND METHODS

2.1. Investigated Area

2.1.1. Location

The area under study lies 12 km SSW of Uppsala, Sweden, within 1 km southwest of the shore of Dalby Bay (Dalbyviken), which is one of the minor bights of the northern part (Ekoln) of Lake Mälaren (Fig. 2). The geographical co-ordinates are 59°46'36"N, 17°33'48"E. The area is covered by the map Ekonomisk karta över Sverige, 'EKS', 11 H 5j, Västeråker (1982). The group of field islands (mean size 256 m^2) is contained within an area of 1.5 km^2 in a patchy agricultural landscape with fields, pastures, and coniferous forests. The locality lies c. 25 m above sea level (Fig. 2 and 4b).

For this study I collected data from 25 field islands, 9 'field peninsulas', and 11 mainland sites (see Fig. 2 and Table 1). The area of the islands ranged from 10 m^2 to 7192 m^2. A cover-abundance list of all observed species is available upon request at the Department of Ecological Botany or from the author.

The area belongs to the northern central-European flora province (Strasburger, 1983) and to the temperate flora zone (Strasburger, 1983) or the boreo-nemoral zone (Walter, 1984).

2.1.2. Physical geography of the area

The investigated area is part of the fissure valley landscape of eastern Svealand (Naturgeografisk Regionindelning av Norden, 'NRN', 1984). The primary rocks are different kinds of gneiss and granites. After the last (Vistula) ice age (25 ka BP), the region was depressed and covered by the Baltic Sea (or rather Litorina Sea) until the 5th century BC (Vägvisare till Naturen i Uppsala Län, 1982). As a consequence from the
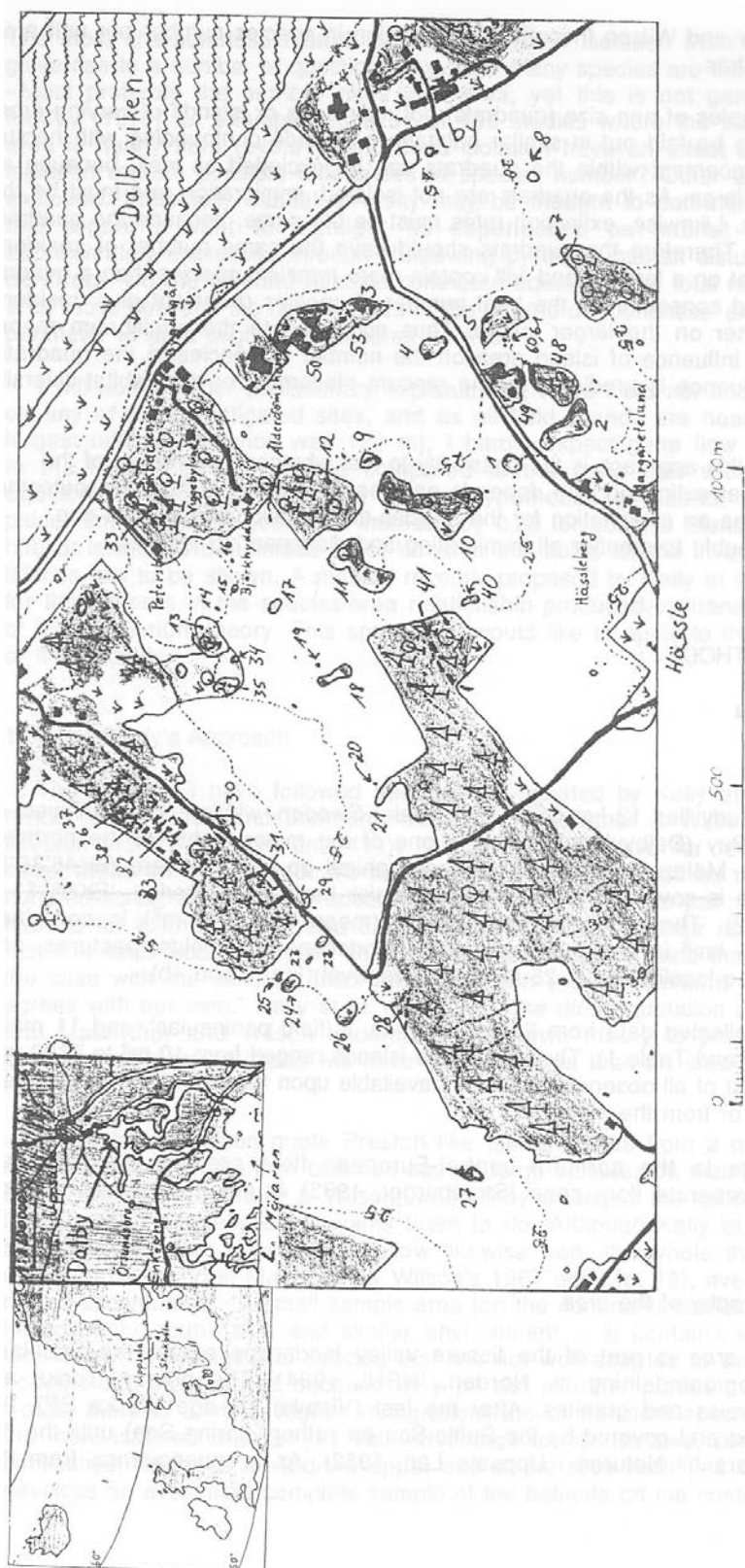
Fig. 2

Location of the study area and map of the field islands, peninsulas and mainland sites (numbered).

Islands 48 and 49 were seperated 5 years ago (1985) and the original island has the number 97. Peninsula 53 comprises sites 50 and 3.

Legend: \|/ grassland, meadow, pasture; t coniferous forest; P deciduous forest; ⋯25⋯ elevation level; ≈ water; — == path, street; (no hatching) arable land.

Field islands

NR	Stot	Atot	lgAtot	BOULDER	TREE	INFL	DISTor	DISTmean	DISTicn	Scn	Acen	lgAcen	Scmnr	Asmma	Sma	Amea	Sfar	Afor	QUSYST1	QUSYST2	QUSYST3	QUSUBJ1	QUSUBJ2	QUSUBJ3	Atot	lgAtot	NR
1	89	513	2.710	5	0	1	70	260	70	74	427.6	2.631	69	85	70	392.6	16	35	24	21	.	19	.	.	513	2.710	1
2	111	3097	3.491	5	8	1	10	160	10	91	2850.0	3.455	51	247	80	1429.8	50	1420	14	12	.	19	.	.	3097	3.491	2
4	65	760	2.881	40	2	1	90	260	90	60	647.3	2.811	40	112	56	631.3	19	16	14	22	.	21	.	.	760	2.881	4
5	125	3005	3.478	5	9	1	40	80	40	96	2771.8	3.443	83	233	91	2376.8	46	395	19	15	.	15	.	.	3005	3.478	5
8	18	13	1.124	40	0	3	120	140	120	10	2.6	0.422	16	11	10	2.6	0	0	.	.	.	.	.	.	13	1.124	8
9	83	472	2.674	30	5	1	30	360	30	66	387.9	2.589	52	85	61	301.1	33	87	10	26	.	16	.	.	472	2.674	9
10	111	7192	3.857	5	8	1	50	300	50	87	6760.3	3.830	82	432	68	1672.9	65	5087	11	15	.	16	.	.	7192	3.857	10
11	93	3314	3.520	5	7	1	30	210	30	79	3037.3	3.482	62	277	70	2421.3	47	616	13	14	.	15	.	.	3314	3.520	11
14	46	84	1.924	25	0	2	20	70	20	33	50.0	1.699	36	34	33	50.0	0	0	11	14	.	.	.	.	84	1.924	14
15	34	68	1.829	30	8	2	30	140	30	29	36.5	1.562	16	31	29	36.5	0	0	17	22	.	.	.	.	68	1.829	15
16	30	88	1.944	50	5	3	30	140	30	20	53.0	1.724	25	35	20	53.0	0	0	15	.	.	.	.	.	88	1.944	16
17	39	180	2.256	50	0	1	90	90	90	37	123.8	2.093	26	57	37	123.8	0	0	17	17	.	15	.	.	180	2.256	17
18	77	730	2.863	75	5	2	50	125	50	72	602.2	2.780	41	128	57	156.0	38	446	22	27	.	25	.	.	730	2.863	18
19	21	40	1.602	80	0	3	20	120	20	10	16.0	1.204	18	24	10	16.0	0	0	7	.	.	.	.	.	40	1.602	19
20	14	10	1.000	80	0	3	10	250	10	7	1.4	0.131	14	9	7	1.4	0	0	.	.	.	.	.	.	10	1.000	20
22	42	107	2.027	40	5	3	30	230	30	27	49.5	1.695	33	57	27	49.5	0	0	5	17	.	16	.	.	107	2.027	22
23	16	15	1.174	60	0	2	30	230	30	7	1.8	0.243	16	13	7	1.8	0	0	.	.	.	.	.	.	15	1.174	23
24	76	384	2.584	20	5	1	40	230	40	68	299.6	2.477	39	84	49	92.6	52	207	23	10	.	20	.	.	384	2.584	24
25	51	187	2.271	10	5	2	15	220	15	40	130.5	2.116	28	56	26	60.5	30	70	17	15	.	.	.	.	187	2.271	25
26	65	748	2.874	5	3	1	40	300	40	57	642.9	2.808	32	106	37	364.9	33	278	9	8	.	19	.	.	748	2.874	26
27	47	423	2.626	15	5	2	60	300	60	35	345.1	2.538	21	78	25	241.1	19	104	11	9	.	.	.	.	423	2.626	27
40	71	254	2.404	10	5	2	20	250	20	64	171.5	2.234	45	82	63	103.5	21	68	24	24	.	23	.	.	254	2.404	40
48	.	.	.	5	9	1	100	100	100	.	2624.0	3.419	.	.	0	0.0	57	2624	.	.	.	.	.	.	.	.	48
49	117	3508	3.545	5	8	1	100	150	100	99	3264.6	3.514	76	243	94	2249.7	44	1015	25	16	.	18	.	.	3508	3.545	49
60	17	47	1.672	70	0	2	20	130	20	13	23.0	1.362	14	24	13	23.0	0	0	7	.	.	.	.	.	47	1.672	60
61	48	78	1.889	40	0	2	10	130	10	31	40.5	1.607	40	37	31	40.5	0	0	22	22	13	.	.	.	78	1.889	61
97	123	4740	3.676	5	8	2	.	.	.	.	4339.8	3.637	.	400	94	700.9	61	3639	25	16	.	18	.	.	4740	3.676	97

Peninsulas

NR	Stot	Atot	lgAtot	BOULDER	TREE	INFL	DISTor	DISTmean	DISTicn	Scn	Acen	lgAcen	Scmnr	Asmma	Sma	Amea	Sfar	Afor	QUSYST1	QUSYST2	QUSYST3	QUSUBJ1	QUSUBJ2	QUSUBJ3	Atot	lgAtot	NR
3	105	1790	3.253	5	3	2	30	150	.	87	1641.6	3.215	64	148	69	1215.6	40	426	15	13	.	22	.	.	1790	3.253	3
7	83	246	2.390	10	5	1	0	0	.	68	204.4	2.310	48	41	68	204.4	0	0	15	17	.	21	.	.	246	2.390	7
12	114	12291	4.090	10	5	1	0	200	.	95	11892.9	4.075	75	398	64	361.0	68	11532	14	17	.	18	18	21	12291	4.090	12
13	96	2311	3.364	30	5	1	70	60	.	79	2164.7	3.335	58	146	56	273.0	66	1892	18	13	.	18	.	.	2311	3.364	13
21	71	714	2.854	10	5	2	0	240	.	63	607.0	2.783	41	107	36	96.0	61	511	13	17	.	.	.	.	714	2.854	21
29	51	88	1.944	75	2	2	0	140	.	44	62.0	1.792	31	26	42	58.0	9	4	25	22	.	17	.	.	88	1.944	29
30	76	1028	3.012	10	5	1	0	0	.	63	937.7	2.972	41	90	53	573.7	41	364	22	18	.	22	.	.	1028	3.012	30
50	114	6671	3.824	5	8	1	0	110	.	95	6382.2	3.805	69	289	83	3092.2	61	3290	12	7	.	16	.	.	6671	3.824	50
53	140	8461	3.927	5	8	1	0	110	.	120	8023.8	3.904	95	438	103	4307.8	72	3716	12	7	14	16	22	.	8461	3.927	53

Mainland

NR	Stot	Atot	lgAtot	BOULDER	TREE	INFL	DISTor	DISTmean	DISTicn	Scn	Acen	lgAcen	Scmnr	Asmma	Sma	Amea	Sfar	Afor	QUSYST1	QUSYST2	QUSYST3	QUSUBJ1	QUSUBJ2	QUSUBJ3	Atot	lgAtot	NR
28	78	327	2.515	5	3	1	0	350	.	75	298.0	2.474	28	29	42	50.0	62	248	17	27	.	.	.	.	327	2.515	28
31	62	876	2.942	20	5	1	0	100	.	40	839.0	2.924	40	37	26	240.0	35	599	9	8	.	6	.	.	876	2.942	31
33	50	396	2.598	5	9	1	0	100	.	50	396.0	2.598	0	0	0	0.0	0	396	.	.	.	.	.	.	396	2.598	33
34	57	96	1.984	25	0	1	15	0	.	46	58.5	1.767	41	38	46	58.5	0	0	27	19	.	20	.	.	96	1.984	34
35	76	434	2.637	50	8	2	40	0	.	59	347.3	2.541	52	87	51	281.3	24	66	17	19	.	15	.	.	434	2.637	35
36	75	1161	3.065	5	7	1	0	0	.	75	1161.0	3.065	0	0	73	1011.0	41	150	19	15	.	11	20	.	1161	3.065	36
37	50	138	2.140	25	5	1	0	0	.	50	138.0	2.140	0	0	27	64.0	0	74	7	13	16	.	.	.	138	2.140	37
38	64	144	2.158	0	8	1	0	0	.	64	144.0	2.158	0	0	64	144.0	0	0	24	28	.	36	.	.	144	2.158	38
41	103	7002	3.845	0	5	2	0	230	.	99	6773.3	3.831	53	229	69	700.9	78	6072	20	12	.	22	.	.	7002	3.845	41
82	22	100	2.000	0	0	1	0	0	.	22	100.0	2.000	0	0	22	100.0	0	0	13	.	.	.	.	.	100	2.000	82
83	73	10730	4.031	5	0	1	0	0	.	73	10729.7	4.031	0	0	73	10729.7	0	0	13	22	11	.	.	.	10730	4.031	83

Table 1

Summery of the basic data of all sites.

Area is measured in [m^2], distance in [m], BOULDER in per cent, TREE COVER in a 10-degree cover-abundance scale, and INFLUENCE in a 3-degree scale.

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glaciation the region is characterized by series of terminal moraines (De Geer moraines), long and large eskers, and clay-filled depressions. Bare rock occurs frequently. The climate is favourable and spring comes earlier than in neighbouring regions. Annual precipitation is low (c. 500 mm/m^2 [Sjörs,1967]). The growing season (threshold +5°C) is approximately 180 d long (Tuhkanen, 1980). Arable land is common in the region, but is often interspersed with forests. The vegetation is rather variable: on bare rock and boulders there will be a lichen type pine forest (Naturtyper i Norden, 1984) and in agricultural areas spruce forests and broad-leaved deciduous forest (NRN,1984), both with a herb-rich field layer. Moreover, meadows and pastures are present.

The immediate vicinity (Fig. 2) of the investigated area consists of arable land, open pastures, grazed forests and ungrazed coniferous forests with mainly planted Norway spruce (*Picea abies*), but Scotch pine (*Pinus sylvestris*) rather on places with thin soil. Deciduous trees, mainly oak (*Quercus robur*), rowan (*Sorbus aucuparia*), birch (*Betula pendula* and *B. pubescens*) and juniper (*Juniperus communis*) are confined to lighter parts of the forests.

I chose this particular group of field islands because their number is high and they are so near to each other that differences in the local climate can be assumed to be negligible. They display a broad range in size and all are ungrazed. In addition, practical advantages (e.g. short distance from Uppsala, easily accessible) were in favour of them.

2.1.3. Local Recent History

Maps from 1743 (Geometrisk Charta....) and 1860 (Karta...Wiggeby) for the NW part (Dalby-Viggeby) and from 1880 (Karta...Dalby Gård) for the NE part (Dalby) which were drawn for the planning of farmland consolidations show that the changes in the landscape under the last 110 to 200 years were small (Fig. 3, 4). Most of the fields from the late 19th century are still in use, except for the land comprising sites 34 and 35 which was turned into a pasture before 1951 (EKS,1953) (Fig. 4a). The open pastures remained unchanged. There is no information however as to the grazed forests. The (grazed?) forest in the southern part of the study area extended until 1860 farther to the west and included field islands 26 and 27. In the time between 1791 and 1860 some parts were turned into fields and sites 20 and 21 became isolated from the forest. After 1860 islands 26 and 27 were separated from this forest as well. Only a path still connects field island 27 to the forest till at least 1953. The legend for a 1791 map (Charta...) shows the western part of the southern forest to be ungrazed, in contrast to the eastern part according to the map from 1743 (Geometrisk charta...Häßle By). From the map from 1860 for the western part of this forest one learns that it was a mixed forest. Between 1860 and 1951 the northern side of the forest was straightened and the field between island 20 and the forest was allowed to regrow (Fig. 4a).

The north-eastern part of the investigation area is covered by a map from 1880 (Karta...Dalby Gård, Fig. 3) and by one from 1913 (Karta...Dalby gård). Assuming that the land surveyors plotted conscientiously, one notices that after thirty years on field islands 2, 5, and 10 trees had grown up, which could indicate that they were grazed less inten-sively. In the surveyor's annotations from 1880 all field islands are called 'mounds' (Sw. 'backe'), but still 1913 they are refered to as wood and pasture land ('skogs- och betesmark'). Since more than a hundred years ago (for the north west part I can state this for the time since 1791), the field islands existed in nearly the same shape as today. Improved ploughing technique however made their shapes rounder by razing the corners, and bights were allowed to overgrow. For the same reason some field islands became united, because the 'sound' between them was too narrow for the broader, more modern ploughs. Two constitute now no. 18 and two others no. 4, in the near future islands 60

and 61 might become one. Until five years ago, in 1985, the two field islands 48 and 49 were a single one (no. "97") and from field island 10's south side a 500 m² ledge was removed.

150 years ago maybe even field island no. 2 belonged to field island 48/49: the passage between no 48 and 2 is narrow and on both sides of the passage grow aspens (*Populus tremula*), which on other field islands indicate an earlier, grave disturbance.

On the 1880 map a rectangular property of arable land, 860 m² in size, is plotted on field island 49 parallel to the road. On this field island I found an abundance of pea trees (*Caragana arborescens*, an introduced garden species [Lid, 1987]), growing like a hedge on the east side, and an overgrown 'hedge' of *Prunus spinosa* as well. In the field island's centre there were plum and apple trees (*Prunus domestica* and *Malus domestica*), several fragrant ornamental rose bushes (*Rosa rugosa*, also an introduced species [Lid, 1987]), and an overamount of fly honeysuckle (*Lonicera xylostea*). Except on field island 49 *Caragana arborescens* was only found on the neighbour field island 5 and *Rosa rugosa* on islands 2 and 5, but neither are found on any other field island or site in the investigated area else. From these indices I conclude that there was a dwelling on this field island before 1860 or that it was used as a kitchen garden.

2.2. Habitat Types

Following the propositions of MacArthur & Wilson (1963, 1967) and Kelly et al. (1989) the field islands had to be divided into distinct and homogeneous habitats, that are similar between the islands. After two preliminary surveys in May 1990, I decided to discern three habitats: margin, meadow, and forest. 'Meadow' and 'forest' should in this context only be understood as convenient labels for two vegetation categories that are mixtures of the phytosociologists' associations. I laid the quadrats in the meadow habitat, because it was the only one that was present on all islands. The margin was not suitable because of its heterogeneity and its linear shape.

I defined the margin as the area that extends 1.0 m inwards from the line composed of the deepest points in the outermost (seen from the field), recent plough furrow or otherwise tilled depression (e.g. a draining ditch). This means that a ditch sometimes belongs with both slopes to the margin (and thereby to the field island) and sometimes, when it was hollowed out recently, with only the inner one. This did however not affect the number of species in the margin area as all species grew on both slopes. 'Recent' means here, that the traces have not yet been covered completely by vegetation and not planed out by erosion.

The margin vegetation consists of mainly (c. 80% cover) grasses (most common: *Agropyron repens*, *Alopecurus pratensis*, *Phleum pratense*, *Dactylis glomerata*, *Agrostis tenuis* and *A. stolonifera*) and some herbs (c. 20% cover) (mostly: *Anthriscus sylvestris*, *Achillea millefolium*, *Geum urbanum*, *Galium album*, *G. boreale*, *Taraxacum officinale*, *Cirsium arvense*, *Matricaria maritima*, *Trifolium pratense*, *Veronica chamaedrys*, *Vicia cracca*, and *Hypericum maculatum*). Typical ruderals like *Fumaria officinalis*, *Euphorbia helioscopia*, *Urtica dioica*, *Myosotis arvensis*, *Polygonum persicaria* , *P. aviculare*, and *Galium aparine* were rare (<5%).

On light parts where a forest is missing, the field islands' centre displays a variety of herbs between the dominant (c. 60% - 70%) grasses, reminding of meadows (grasses: *Alopecurus pratensis*, *Phleum pratense*, *Dactylis glomerata*, *Agrostis tenuis*, *A. stolonifera*, *Poa angustifolia*, *Festuca rubra*, *Avenula pratensis*, *Deschampsia flexuosa*; herbs: *Anthriscus*

Fig. 3
Historical maps of the study area.
Hatched areas are ungrazed forests, plain areas are fields, the tree symbols were amended for clarity. The maps are reproduced in reduced size. NW-part: Karta öfver alla egorne till Wiggeby..., 1860; NE-part: Karta öfver alla ägorna till kronohemmet Dalby gård..., (1880); S-part: Geometrisk Charta ut af Häßle By... (1743).

Fig. 4
Recent economical maps of the study area
Top: map from 1953 , bottom: map from 1982 (Ekonomisk karta över Sverige 11H hj Västeråker, 1st edition 1953, 2nd edition 1982)

sylvestris, *Achillea millefolium*, *Galium album*, *G. boreale*, *G. verum*, *Filipendula vulgaris*, *Trifolium pratense*, *Hypericum maculatum*, *Geum urbanum*, *Potentilla argentea*, *Fragaria vesca*, *Veronica chamaedrys*, *Vicia cracca*, *Stellaria media*, *Viola spp.*, *Rumex acetosella*, *Primula veris*). Most 'meadows' include shrubs and trees (shrubs: *Juniperus communis*, *Prunus spinosa*, *Rosa canina agg.*; trees: *Pinus sylvestris*, *Juniperus communis*, *Quercus robur*, and *Sorbus aucuparia*). Where the soil is thin, other species take over: *Festuca ovina*, *Deschampsia flexuosa*, *Poa compressa*, *Anthoxanthum odoratum*; *Saxifraga granulata*, *Sedum sexangulare*, *Scleranthus annuus*, *Lychnis viscaria*, *Campanula rotundifolia*, *Luzula pilosa*, *Pseudolysimachia* (=*Veronica*) *spicata*, *Acinos arvensis*, *Rumex tenuifolius*, *Hieracium pilosella*, and *Viola arvensis*. Sometimes *Calluna vulgaris* and from the field island's 'forest' *Convallaria majalis*, *Rubus saxatilis*, *Vaccinium myrtillis* and *Vaccinium vitis-idaea* scatter in. In contrast to the 'forest' habitat (see below) I defined 'meadow' as that part of the field island that neither is forest nor margin by the given definitions.

'Forest' I called that part of a site, larger than 1 m², whose tree-layer (>2 m) covered the ground 90% - 100% and whose field-layer (excluding mosses and lichens) covered the soil less then 90%. The height-limit for the tree-layer caused sometimes big-grown bushes to be included in the tree-layer and some forest parts are in fact *Rosa* or *Prunus spinosa* 'forests'.

The forests on the field islands are very heterogeneous, however, the larger they are the more they resemble a 'typical' forest. Pine (*Pinus sylvestris*), oak (*Quercus robur*) and rowan (*Sorbus aucuparia*) often dominate the tree-layer. Other tree species that occur regularly are aspen (*Populus tremula*), maple (*Acer platanoides*), birch (*Betula pendula*), bird's cherry (*Padus avium* [=*Prunus padus*]), Swedish whitebeam (*Sorbus intermedia*), and juniper (*Juniperus communis*). Spruce (*Picea abies*) is rare and only found on the largest islands. In the shrub-layer (0.5 m to 2 m) one finds most of the tree species, but oak and pine less and rowan more frequently than in the tree-layer. Moreover, there are *Prunus spinosa*, *Juniperus communis*, *Rosa canina agg.*, *Rubus idaeus*, *Ribes uva-crispa*, and *Ribes alpinum* as the most common bush species.

Typical species in the forests' field layer are the grasses *Deschampsia flexuosa*, *Dactylis glomerata*, *Phleum pratense*, *Agrostis tenuis*, *Agrostis stolonifera*, and *Poa angustifolia*, and the herbs *Geum urbanum*, *Anthriscus sylvestris*, *Galeopsis tetrahit*, *Galium album*, *Galium boreale*, *Urtica dioica*, *Rumex acetosella*, *Polygonatum odoratum*, *Actaea spicata*, *Rubus saxatilis*, *Paris quadrifolia*, and *Vaccinium vitis-idaea*.

Of course, the border between the habitats is not sharp and many species scatter into adjacent habitats.

Typical pasture and meadow species indicate (Ellenberg, 1984; Sjörs, 1967; Inventering av Ängs- och Hagmarker, 1987) that most field islands were grazed (*Juniperus communis*, *Rhamnus catharticus*, *Prunus spinosa*, *Berberis vulgaris*, *Pinus sylvestris*; *Agrostis tenuis*, *Anthoxanthum odoratum*, *Achillea millefolium*, *Campanula rotundifolia*, *Hieracium pilosella*, *Leucanthemum vulgare*, *Pimpinella saxifraga*, *Polygala vulgaris*, *Potentilla erecta*, *Stellaria graminea*, *Festuca rubra*, *Trifolium pratense*, *Phleum pratense*, *Poa pratensis*, *Plantago lanceolata*, *Taraxacum officinale*) or cut (*Anthoxanthum odoratum*, *Campanula rotundifolia*, *Dianthus deltoides*, *Filipendula vulgaris*, *Helianthemum nummularium*, *Melampyrum cristatum*, *Pimpinella saxifraga*, *Polygala vulgaris*, *Saxifraga granulata*, *Serratula tinctoria*, *Pseudolysimachium* (=*Veronica*) *spicata*, *Viola hirta*, *Viola canina*, *Festuca rubra*, and *Leucanthemum vulgare*).

2.3. Fieldwork

2.3.1. Searching the Field Islands

I visited all field islands, peninsulas, and mainland sites, except no. 48, 49, 50, 82, and 83, in May/June 1990 and visited all in July/August. Depending on the site's area it took me 10 minutes on the smallest (10 m^2) and four to five hours on the biggest ones (12 000 m^2) to search them for all species. On all field islands and peninsulas I first searched the margin, determined then the borderline for the forest -if present- scrutinized the forest and finally screened the meadow. By walking to and fro I advanced within forest and meadow and covered thus the whole area. I listed the species separately for each habitat on my first visit and used the lists to compile a check-list for the second visit, thus having the possibility to control the data from the first visit. I measured the dimensions of the forest with a 50-m-measuring tape when appropriate or else plotted the measured contours of the forest into a 1:4000 map. Sometimes it was easier to measure the meadow. When the size of the field island allowed, I determined also the extension of the whole site, using simple geometric shapes (rectangle, triangle, circle, ellipse) as a model.

2.3.2. Laying out the Quadrats

Finally, I established the sample quadrats. I chose the size of 16 m^2 (4m·4m) in order to be able to lay out at least one quadrat even on the smaller field islands. For the same reason I confined myself to lay the quadrats on the meadow which was found on all islands. Where possible I laid out three quadrats. The centre point for two quadrats was found by following a set of rules: 1. Start from the southernmost corner of the meadow. 2. Measure the distance in northern direction from that point to the next habitat border. 3. The centre point of the quadrat is placed on the half of this distance and so that one of the quadrat's diagonals follows the measuring tape. 4. If the features of the site are such that following the preceding rules does not lead to a point where a 16-m^2-quadrat could be placed, the starting point has to be moved to the corner in the a) north, b) the west, c) the east d) the non-cardinal directions clockwise. 5. the same rules apply to the second quadrat, starting with the northern corner of the same meadow or the southern corner of another meadow with considerable size. 6. On the smaller field islands the alignment has to be fitted to the field island.

The third, 'subjective', quadrat, as opposed to the 'systematic' quadrats above, was used to cover parts of the meadow that differed floristically from the first two and seemed to contain underrepresented species. In three cases, no. 12, 36, and 52 (all are mainland sites) I took more than one 'subjective' quadrat to cover the variety in vegetation. In two small islands the total meadow area could be covered by three quadrats, which I classified as 'systematic'.

I searched the quadrats intensively for species and was able to detect on the largest field islands two to four species that I had overlooked when searching the whole site, implying a possible underestimation of ≤5% for the number of species per habitat.

2.3.3. Habitat Variables

As the amount of bare rock, tree cover on the meadow, and intensity of human influence are possible factors to affect species diversity, I estimated the part of the total area covered by bare (total absence of vascular plants) rock and boulder in percent,

estimated tree cover in the Braun-Blanquet scale, which I transformed later to facilitate computer analysis (absent ⇒ 0, r ⇒ 1, + ⇒ 2; 1 ⇒ 3, 2 ⇒ 5, 3 ⇒ 7, 4 ⇒ 8, 5 ⇒ 9; see Westhoff & van der Maarel, 1979), and estimated human influence in an ordinal, rather subjective scale (1 - little, 2 - moderate, 3 - strong). Strong influence was indicated by disturbed soil, many annuals, nitrophiles and other 'weed' species. Moderate influence could be indicated by minor parts of the field island being heavily disturbed, recently deposited stones, or other deposited material (tools, sticks, plastic bags, etc.). Little influence included wood being taken from the forests and on the margin influence by agriculture.

I called the respective habitat variables BOULDER, TREECOV(E)R, and INFLUENC(E) (see Table 2).

2.4. Determining Field Island and Habitat Area

After fieldwork I determined the size of all field islands, peninsulas and habitats from maps scaled 1:10 000 (EKS, 1982, Fig. 4b [from aerial photographs]) and 1:4000 (Karta...Dalby Gård, 1880; Karta...Wiggeby, 1860 [both from geodetic surveys]) with a digitizing pad. For some islands I had to correct the shape (see 2.1.3. 'Local Recent History') due to changes since the plotting of the maps and I used field measurements to enter the deviations in the map. In order to minimize measurement errors (the island contours have to be followed with a kind of 'mouse'), I repeated the area measurements once and in some cases twice. Next I compared the results from the different maps with the field measurements. I excluded results that deviated from the field measurements by more than 10% and prefered when I lacked field measurements the results from the 1:4000 maps. From the remaining results and field measurements I calculated the arithmetic mean as the final value for area. The smallest field islands had to be drawn in scale 1:100 on paper and their area was calculated by fitting smaller triangles to it.

The margin area for islands with more than 50 m in diameter was calculated as perimeter length multiplied by 1 m. For calculating the area of the habitat for which I did not have field measurements, I subtracted the margin area and the area of the third habitat from the total area. For the smaller field islands I used the following formulae to calculate the margin area taking into account that just multiplying by 1 m will over-estimate the margin area:

circle : $M = \pi (2r-1)^2$ (where r is radius)
ellipse: $M = \pi (a+b-1)^2$ (where a and b are the half-axes)
rectangle: $M = 4 (a+b-1)^2$ (where a and b are the halves of the sides).

2.5. Measures of Isolation

The source of dispersal differs for different species. I assume the surrounding forests as the source for all tree species and several of the forest species (e.g. *Actaea spicata* or *Paris quadrifolia*). Most grasses and herbs will come from the grasslands in the vicinity. I measured with a ruler on a 1:10 000 map the shortest distance to the next grassland ('DISTmea'), be it on the mainland or a larger field island, and the distance to the nearest forest ('DISTfor'), again either on the mainland or on a larger field island whatever was nearer. In case the shortest distance from a field island to the mainland or a larger island was decisive, I took the minimum value of DISTmea and DISTfor for each field island and called this the minimum distance ('DISTmin').

Table 2
Short definitions of habitats and habitat variables (capital letters)

margin	1 m - broad margin of an field island or a field peninsula
forest	tree cover >90%, field layer cover <90%
meadow	neither margin nor forest
central	meadow + forest
total	margin + forest + meadow
BOULDER	percentage cover of bare rocks
TREECOVER	tree cover on the meadow, 10-degree cover-abundance scale
INFLUENCE	degree of human disturbance, three-degree scale
DISTfor/ DISTmea	distance to the nearest forest or meadow on island or mainland
DISTmin	smallest distance to either forest or meadow
A_{mar}/A_{tot}	a measure for the degree of roundness of an island, a perfectly circular island has the value $(2r-1)^2/r^2$

2.6. Statistical Analysis

Statistics were calculated with the SAS programme package (SAS Institute Inc., 1985).

The regression of species number in quadrats on island area was done by the G(eneral)L(inear)M(odel) PROCEDURE. I excluded islands 60 and 19 because their meadow parts consisted of bare rock. Their inclusion had violated the assumption of similar habitats. To compare subjective and systematic quadrats I used a t-test and an ANOVA to compare the mean number of species of quadrats on islands, peninsulas, and the mainland.

The CORRELATION PROCEDURE used Pearson correlation coefficients to make a cor-relation matrix including all variables describing species richness, area, island shape, habitat and disturbance, and isolation for the 25 field islands (see list in appendix). S_{for} was set to zero and $lg(A_{for})$ and $lg(S_{for})$ were set to -5 when a forest was missing on an island. In an alternative calculation combinations with these variables were excluded.

I made the procedure STEPWISE carry out linear stepwise regression for $1/S_{tot}$, S_{tot}, and $lg(S_{tot})$ on logarithmically transformed area variables and variables describing habitat, disturbance, shape and distance (the appendix gives an overview about the used variables). The STEPWISE procedure begins with no variables in the model and adds the next variable when the F statistics for a variable to be added is significant at the 15% level (default option). After a variable is added, the procedure looks at all variables already included in the model and deletes any variable that does not produce an F statistic significant at the 15% level (default option) (SAS Institute Inc., 1985). I included

inverse values of area, species number and habitat variables in case hyperbolic or inverse exponential models turned out favourable.

The RMAX (maximum R^2 improvement) option in the STEPWISE procedure tries to find the best (highest R^2-value) one-variable model, two-variable model, and so on. The procedure starts with the variable that produces the highest R^2-value and adds for the two-variable model that variable that yields the greatest increase in R^2. Next the program controls if exchanging one of the variables in the model against one outside the model would increase R^2 even more and chooses the variables that give the highest R^2-value. Comparison begins again until no exchange could increase R^2 and starts over again for the three-variable model. The found models are considered to be the 'best' models, because the program has evaluated all possible variable combinations that might increase R^2 (SAS Institute Inc., 1985). This option provided up to five parameters (limited by the chosen option RMAX=4) for the transformed power and logarithmic equations, and I used the results to see which relative importance habitat descriptors had.

I used a R_a^2-table, calculated by the procedure RSQUARE, to compare the different models quickly, for closer examination I also inspected the residual plots. For some combinations and the non-linear models I calculated R_a^2 by applying the equation $R_a^2 = 1 - \left((1 - R^2) \cdot \frac{n-1}{n-k} \right)$, with n = number of observations and k = number of parameters (Ekbohm & Rydin, 1990).

For all transformed power models with maximal three parameters and simple hyperbolic, inverse exponential, and logistic models I let the NLIN procedure produce a non-linear regression curve on the untransformed models.

In order to find the best fitted regression with maximal three parameters I inspected the residual plots of all corresponding power, transformed power, exponential and non-linear equations and compared their R_a^2-values (Ekbohm & Rydin, 1990). The best model $\lg(S_{tot}) = c + z \cdot \lg(A_{cen}) + b \, BOULDER^2$ was subject to further improvement measures. I excluded outliers (no. 60 and 18), replaced field island 49 against 97 (i.e. the combination of islands 48 and 49 as they were 5 years ago), and divided the curve in different regions that corresponded with deviating habitat composition. I tried again with STEPWISE and plotted the residuals. All these measures did not contribute to a substantial better prediction of the number of species. The regressions were executed excluding a model error term.

3. RESULTS

1. All descriptors for area, species richness, habitat, and island shape (A_{mar}/A_{tot}) are significantly ($p<0.005$) correlated with each other. The correlation between area and species number was constantly high ($r>0.7$) in whatever way these variables were expressed. Except for combinations with INFLUENCE or A_{mar}/A_{tot} the correlations are positive. When for combinations with S_{for}, $\lg(S_{for})$, and $\lg(A_{for})$ islands without forests were excluded from calculating the matrix, these variables were significantly only cor-related to $\lg(S_{for})$, S_{for}, $\lg(A_{mar})$, $\lg(A_{for})$, $\lg(A_{cen})$, $\lg(A_{tot})$, and TREECOVER (Table 3).

2. The distance variables were not significantly correlated ($p>0.05$) to species richness, neither for the whole field islands nor for the quadrats. TREECOVER and INFLUENCE were also uncorrelated with each other (Table 3).

	Stot	Scen	Smar	Sfor	Smea	lg(Stot)	lg(Atot)	lg(Acen)	lg(Amar)	lg(Afor)	lg(Amea)	INFLUENCE	TREECOVER	BOULDER	Amar/Atot	DISTfor	DISTmea	QU_ALL
Stot	1.00000	0.98739	0.93882	0.65832	0.97094	0.95705	0.93915	0.91803	0.92745	0.66504	0.89988	-0.76406	0.70208	-0.72637	-0.85997	0.13300	0.15545	0.32544
	0.0000	0.0001	0.0001	0.0105	0.0001	0.0001	0.0001	0.0001	0.0001	0.0095	0.0001	0.0001	0.0001	0.0001	0.0001	0.5262	0.4581	0.1124
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
Scen	0.98739	1.00000	0.90138	0.63792	0.97686	0.96140	0.94444	0.92928	0.93364	0.63784	0.90457	-0.80056	0.68727	-0.70696	-0.88665	0.17848	0.16603	0.38564
	0.0001	0.0000	0.0001	0.0141	0.0001	0.0001	0.0001	0.0001	0.0001	0.0141	0.0001	0.0001	0.0001	0.0001	0.0001	0.3933	0.4277	0.0569
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
Smar	0.93882	0.90138	1.00000	0.50398	0.91934	0.87423	0.84923	0.82078	0.84125	0.50117	0.82290	-0.67598	0.56634	-0.66226	-0.74211	0.16435	0.12100	0.31162
	0.0001	0.0001	0.0000	0.0661	0.0001	0.0001	0.0001	0.0001	0.0001	0.0679	0.0001	0.0002	0.0032	0.0003	0.0001	0.4324	0.5645	0.1294
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
Sfor	0.65832	0.63792	0.50398	1.00000	0.41916	0.65122	0.72031	0.71144	0.75392	0.88798	0.47585	-0.42871	0.75951	-0.17517	-0.56896	-0.21626	-0.31062	-0.23906
	0.0105	0.0141	0.0661	0.0000	0.1357	0.0116	0.0037	0.0043	0.0018	0.0001	0.0855	0.1261	0.0016	0.5492	0.0337	0.4577	0.2797	0.4104
	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
Smea	0.97094	0.97686	0.91934	0.41916	1.00000	0.93243	0.89821	0.88339	0.88910	0.43610	0.88657	-0.76636	0.65256	-0.67334	-0.83593	0.20039	0.07914	0.42601
	0.0001	0.0001	0.0001	0.1357	0.0000	0.0001	0.0001	0.0001	0.0001	0.1190	0.0001	0.0001	0.0004	0.0002	0.0001	0.3368	0.7069	0.0337
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
lg(Stot)	0.95705	0.96140	0.87423	0.65122	0.93243	1.00000	0.93605	0.94357	0.94104	0.63854	0.92440	-0.76673	0.67945	-0.76651	-0.92523	0.11889	0.19491	0.36130
	0.0001	0.0001	0.0001	0.0116	0.0001	0.0000	0.0001	0.0001	0.0001	0.0140	0.0001	0.0001	0.0002	0.0001	0.0001	0.5714	0.3505	0.0760
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
lg(Atot)	0.93915	0.94444	0.84923	0.72031	0.89821	0.93605	1.00000	0.99155	0.99295	0.80258	0.97334	-0.78215	0.72124	-0.70413	-0.94591	0.16534	0.20080	0.15786
	0.0001	0.0001	0.0001	0.0037	0.0001	0.0001	0.0000	0.0001	0.0001	0.0006	0.0001	0.0001	0.0001	0.0001	0.0001	0.4296	0.3358	0.4511
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
lg(Acen)	0.91803	0.92928	0.82078	0.71144	0.88339	0.94357	0.99155	1.00000	0.98838	0.79376	0.98508	-0.77698	0.70734	-0.70670	-0.97649	0.15355	0.17716	0.14824
	0.0001	0.0001	0.0001	0.0043	0.0001	0.0001	0.0001	0.0000	0.0001	0.0007	0.0001	0.0001	0.0001	0.0001	0.0001	0.4637	0.3969	0.4795
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
lg(Amar)	0.92745	0.93364	0.84125	0.75392	0.88910	0.94104	0.99295	0.98838	1.00000	0.82985	0.96688	-0.75364	0.73125	-0.69287	-0.93827	0.12789	0.19258	0.16950
	0.0001	0.0001	0.0001	0.0018	0.0001	0.0001	0.0001	0.0001	0.0000	0.0002	0.0001	0.0001	0.0001	0.0001	0.0001	0.5424	0.3564	0.4179
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
lg(Afor)	0.66504	0.63784	0.50117	0.88798	0.43610	0.63854	0.80258	0.79376	0.82985	1.00000	0.56689	-0.26409	0.78283	-0.22660	-0.64838	-0.14605	-0.32556	-0.27507
	0.0095	0.0141	0.0679	0.0001	0.1190	0.0140	0.0006	0.0007	0.0002	0.0000	0.0345	0.3616	0.0009	0.4360	0.0121	0.6183	0.2560	0.3412
	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14	14
lg(Amea)	0.89988	0.90457	0.82290	0.47585	0.88657	0.92440	0.97334	0.98508	0.96688	0.56689	1.00000	-0.77733	0.67534	-0.71257	-0.96496	0.17592	0.13795	0.11156
	0.0001	0.0001	0.0001	0.0855	0.0001	0.0001	0.0001	0.0001	0.0001	0.0345	0.0000	0.0001	0.0002	0.0001	0.0001	0.4003	0.5108	0.5955
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
INFLUENCE	-0.76406	-0.80056	-0.67598	-0.42871	-0.76636	-0.76673	-0.78215	-0.77698	-0.75364	-0.26409	-0.77733	1.00000	-0.37365	0.63310	0.78614	-0.22453	-0.23644	-0.22474
	0.0001	0.0001	0.0002	0.1261	0.0001	0.0001	0.0001	0.0001	0.0001	0.3616	0.0001	0.0000	0.0658	0.0007	0.0001	0.2806	0.2552	0.2801
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
TREECOVER	0.70208	0.68727	0.56634	0.75951	0.65256	0.67945	0.72124	0.70734	0.73125	0.78283	0.67534	-0.37365	1.00000	-0.58916	-0.64033	-0.06779	0.12153	0.17904
	0.0001	0.0001	0.0032	0.0016	0.0004	0.0002	0.0001	0.0001	0.0001	0.0009	0.0002	0.0658	0.0000	0.0020	0.0006	0.7475	0.5628	0.3918
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
BOULDER	-0.72637	-0.70696	-0.66226	-0.17517	-0.67334	-0.76651	-0.70413	-0.70670	-0.69287	-0.22660	-0.71257	0.63310	-0.58916	1.00000	0.69456	-0.12548	-0.29158	-0.14856
	0.0001	0.0001	0.0003	0.5492	0.0002	0.0001	0.0001	0.0001	0.0001	0.4360	0.0001	0.0007	0.0020	0.0000	0.0001	0.5501	0.1573	0.4785
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
Amar/Atot	-0.85997	-0.88665	-0.74211	-0.56896	-0.83593	-0.92523	-0.94591	-0.97649	-0.93827	-0.64838	-0.96496	0.78614	-0.64033	0.69456	1.00000	-0.15666	-0.18714	-0.16364
	0.0001	0.0001	0.0001	0.0337	0.0001	0.0001	0.0001	0.0001	0.0001	0.0121	0.0001	0.0001	0.0006	0.0001	0.0000	0.4546	0.3704	0.4344
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
DISTfor	0.13300	0.17848	0.16435	-0.21626	0.20039	0.11889	0.16534	0.15355	0.12789	-0.14605	0.17592	-0.22453	-0.06779	-0.12548	-0.15666	1.00000	-0.02046	0.23835
	0.5262	0.3933	0.4324	0.4577	0.3368	0.5714	0.4296	0.4637	0.5424	0.6183	0.4003	0.2806	0.7475	0.5501	0.4546	0.0000	0.9227	0.2512
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
DISTmea	0.15545	0.16603	0.12100	-0.31062	0.07914	0.19491	0.20080	0.17716	0.19258	-0.32556	0.13795	-0.23644	0.12153	-0.29158	-0.18714	-0.02046	1.00000	0.04914
	0.4581	0.4277	0.5645	0.2797	0.7069	0.3505	0.3358	0.3969	0.3564	0.2560	0.5108	0.2552	0.5628	0.1573	0.3704	0.9227	0.0000	0.8155
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25
QU ALL	0.32544	0.38564	0.31162	-0.23906	0.42601	0.36130	0.15786	0.14824	0.16950	-0.27507	0.11156	-0.22474	0.17904	-0.14856	-0.16364	0.23835	0.04914	1.00000
	0.1124	0.0569	0.1294	0.4104	0.0337	0.0760	0.4511	0.4795	0.4179	0.3412	0.5955	0.2801	0.3918	0.4785	0.4344	0.2512	0.8155	0.0000
	25	25	25	14	25	25	25	25	25	14	25	25	25	25	25	25	25	25

Table 3

Shortened version of the correlation table for field islands.
A complete enumeration of all variables used in the original table are listed in appendix 1.
First line: Pearson correlation coefficient ('r'), second line: probability for the correlation not deviating from zero, third line: number of observations. When no forest was present on a field island, the number of observations is lower for combinations with forest area (lg(A_{for})) or species richness (S_{for}, lg(S_{for})), because those islands were excluded in these cases. In an alternative calculation S_{for} was set to zero and lg(A_{for}) and lg(S_{for}) were set to -5. The correlations for these combinations were then significant ($p<0.005$).
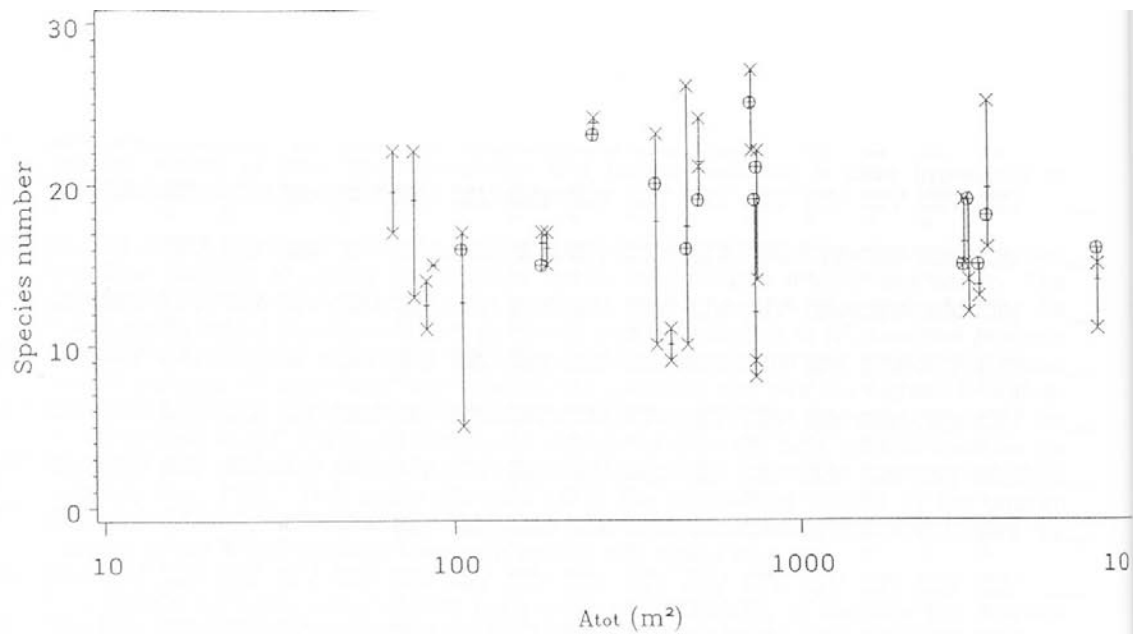
25

Fig. 5

Species number of systematically (X) and subjectively (⊕) laid quadrats of field islands. Mean number of all quadrats of one island is indicated by a bar (−). Regression was insignificant (p>0.1)
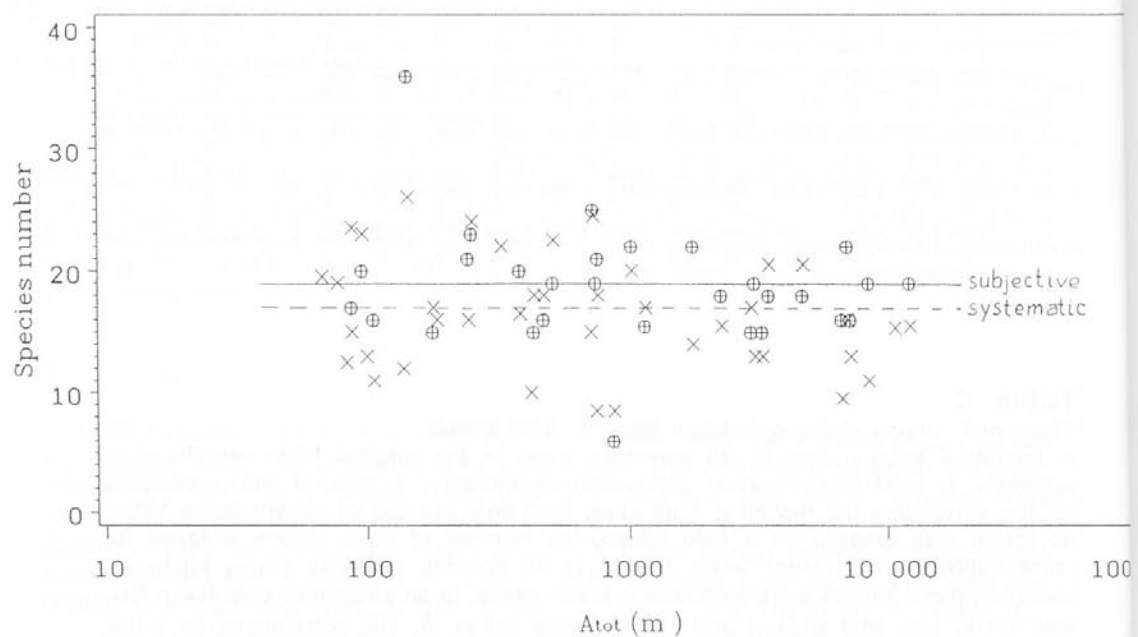

Fig. 5a

Mean species number of systematically (X) and subjectively (⊕) laid quadrats of all sites. Regression was insignificant (p>0.1), but subjective quadrats contain in average two more species than systematic quadrats (t-test, p<0.05)

3. The distance from an island to the nearest forest (DISTfor) was always equal to or smaller than the distance to the nearest meadow (DISTmea), so that DISTmin=DISTfor.

4. The slopes for systematically and subjectively laid quadrats for islands, peninsulas, and mainland sites did not differ much from zero (20 quadrats, R^2 for species number regressed on total area was less than 0.05) (Fig. 5, 6). A paired t-test for the means of species number for field islands showed that the probability for a difference between the quadrat types was insignificant (p=0.19, n=14). As the number of pairs for peninsulas and mainland sites was low, I run a t-test for all sites in one group (n=28). Here the probability for a difference was 0.03: in average there are two species more in subjectively laid quadrats than in systematically laid quadrats (Fig. 5a).

5. There was no detectable difference found for the mean number of species in the quadrats of one site between islands, peninsulas and mainland sites (Fig. 6) by an analysis of variance (F=0.32).
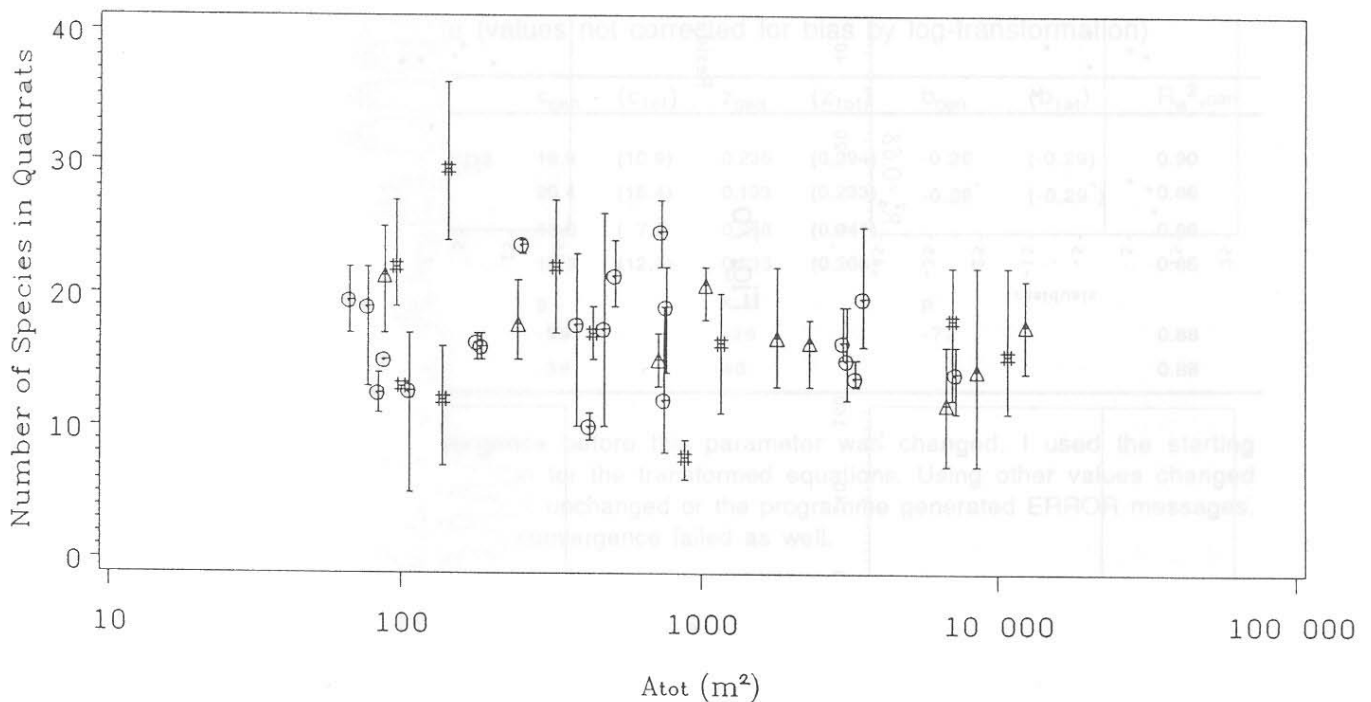
Fig. 6. Average species number in quadrats of field islands (⊙), peninsulas (Δ), and mainland (#). Maximum and minimum values are indicated by bars. The regression equation's fit (R^2) was <0.01 for field island, 0.16 for pensinsulas, and 0.06 for mainland data

6. There is a significant positive correlation between area and species abundance for all habitat areas, the central, and the total sample area.

7. The best (by R_a^2 and residual plot) three-parameter model to predict the number of species on field islands found by stepwise regression with an entry and stay significance of 15% for the variables (see statistical methods, above), and by stepwise regression

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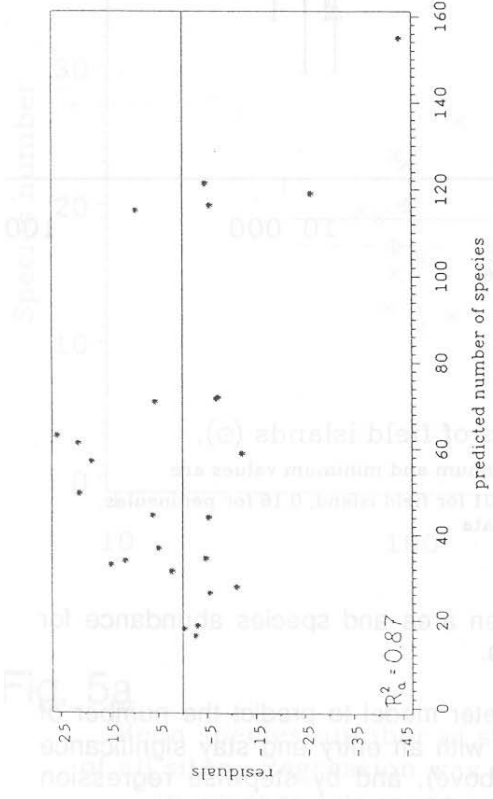
Fig. 7a — Residual plot for $\lg(S_{tot}) = 8 + 0.34 \cdot \lg(A_{tot})$, $R_a^2 = 0.87$
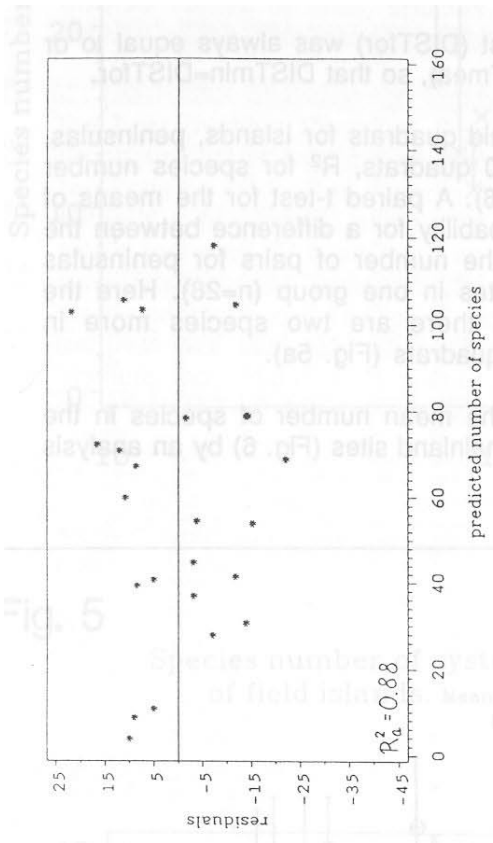
Fig. 7b — Residual plot for $S_{tot} = -36 + 40 \cdot \lg(A_{tot})$, $R_a^2 = 0.88$
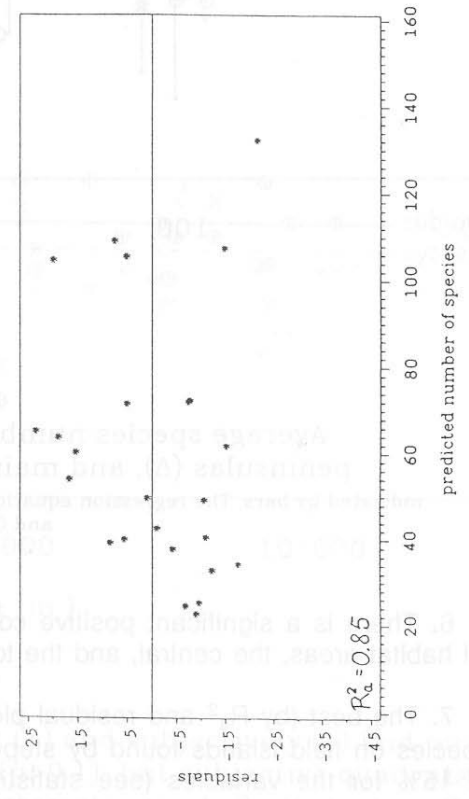
Fig. 7c — Residual plot for $S_{tot} = 12.3 \cdot A_{tot}^{0.27}$, $R_a^2 = 0.85$
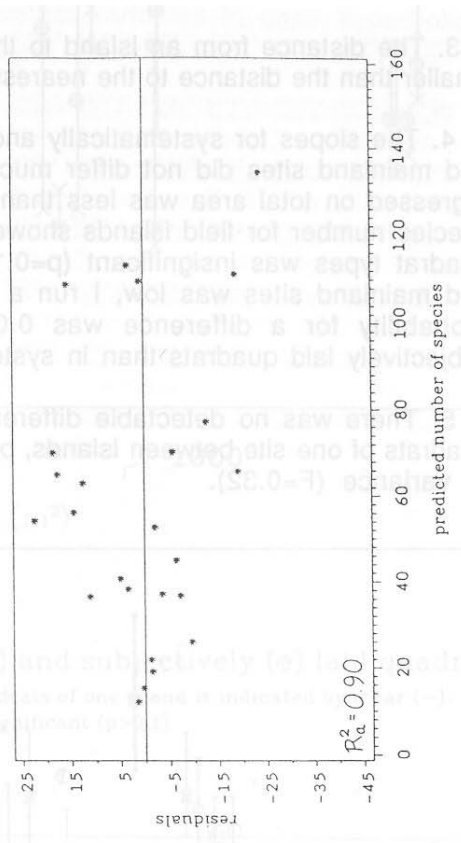
Fig. 7d — Residual plot for $\lg(S_{tot}) = 17 + 0.24 \cdot \lg(A_{cen}) - 0.26 \cdot BOULDER^2$, $R_a^2 = 0.90$

with R^2-max improvement was $lg(S_{tot}) = lg(c) + z \cdot lg(A_{cen}) + b \cdot BOULDER^2$. Best two-parameter model was $lg(S_{tot}) = lg(c) + z \cdot lg(A_{cen})$ and best non-linear model $S_{tot} = c \cdot A_{cen}{}^z$. Using the logarithmic model, best fit was gained by applying the equation $S_{tot} = g + m \cdot lg(A_{cen}) \cdot lg(A_{tot})$. The other factors that RMAX included into the model (INFLUENCE, A_{mea}/A_{tot}, A_{for}/A_{mea}, and $lg(A_{mea})$) did not raise $R_a{}^2$.

The highest $R_a{}^2$ I had achieved was 0.95 for the equation $lg(S_{tot}) = 1.01 + 0.23\ lg(A_{tot}) - 0.23\ BOULDER + 0.0146\ QU\_ALL$

8. The increase of species number with total area was faster on the field islands (z=0.34) than on the peninsulas (z=0.17) or the mainland (z=0.15) (z-values from regression on the transformed power equation)

Table 4.
Synopsis of the best models (values not corrected for bias by log-transformation)

equation	c_{cen}	(c_{tot})	z_{cen}	(z_{tot})	b_{cen}	(b_{tot})	$R_a{}^2{}_{,cen}$
$lgS_{tot}=lg(c)+z \cdot lg(A)+b \cdot BOULDER^2$	16.9	(10.9)	0.235	(0.294)	-0.26	(-0.29)	0.90
$S_{tot}=c \cdot A^z \cdot 10^{b \cdot BOULDER^2}$	20.4	(16.4)	0.193	(0.233)	-0.26*	(-0.29*)	0.86
$lg(S_{tot})=lg(c)+z \cdot lg(A)$	13.0	(7.5)	0.268	(0.341)			0.89
$S_{tot}=c \cdot A^z$	16.3	(12.3)	0.235	(0.268)			0.86
	g		k		p		
$S_{tot}=g+k \cdot lg(A_{cen})+p \cdot lg(A_{tot})$	-59		-26		-73		0.88
$S_{tot}=g+k \cdot lg(A_{tot})$	-36		40				0.88

*) the procedure stated convergence before this parameter was changed. I used the starting parameter value found by regression for the transformed equations. Using other values changed c and z slightly, but b itself remained unchanged or the programme generated ERROR messages. Increasing the demands for stating convergence failed as well.

4. DISCUSSION

I was surprised to find so strong correlations between species richness and area even when the values came from different habitats, for instance between $lg(S_{mea})$ and $lg(A_{mar})$ R^2 was 0.83. This is due to the fact that the habitat areas, especially meadow and forest themselves, are correlated with each other. In a comparison of published reports, Connor & McCoy (1979) report only 119 out of 400 species-area regressions with a better fit than $R^2=0.80$.

4.1. Influence of Distance on Species Richness

There was no correlation between proximity of an island to a source pool and the number of species. The effects of distance can therefore be neglected for the following discussion. This means either that one of the basic assumptions in MacArthur & Wilson's theory is not valid here, or that the distances to the next forest, DISTfor (mean value = 42 m) or the next grassland, DISTmea, (195 m) make no difference for most of the diaspores.

4.2. Relation between Total Island Area and Number of Species in Quadrats

Although the number of species rises with island area, the species number in the quadrats was independent of the island area. As all quadrats were equally sized and lay in the same habitat random placement and habitat heterogeneity can be excluded as an explanation for the species-quadrat relation.

This means that the number of transient species is equal for small and large island quadrats. If now the rate of extinction were dependent on island area, than the species pool, i.e. the total number of species on the island, had to be larger on the smaller islands. But the investigation shows that this is not the case, consequently the rate of extinction is not dependent on island area.

There is now evidence from two results that two of the basic assumptions of MacArthur & Wilson's theory are violated in the field island system: distance is not correlated with species number and extinction is not correlated to area.

This corresponds to Kelly et al. (1989) findings in their species-area study on manuca scrub forests on islands in New Zealand where they could not find a relation between species richness in quadrats and island area although an earlier study had indicated the validity of the equilibrium theory.

Critique regarding the execution of the Kelly-approach might be raised against the possible lack of similarity of the meadow-habitats. Of course it will be nearly impossible that two habitats are identical, but a glance on the correlation table (Table 3) shows that the number of species in the quadrats is not correlated to any of the three habitat variables, thus habitat diversity seems at least not to be responsible for the number of species in quadrats. Another objection could be that the results show that the field islands are not enough isolated from the mainland. This is true as far as field islands are not real islands but habitat islands. However, as I described above, the 'ocean' is uninhabitable for all species but the few annuals, consequently the isolation is sufficient.

4.3. The Best Two-Parameter Model for the Species-Area Curve

As I wrote above, after Gleason (1922) had introduced the logarithmic model, there was an argument between the scientists as to which model –his or Arrhenius' power model- were best. I will take up the question here for this investigation.

I fitted both transformed and untransformed power and the logarithmic model to the data. The R_a^2-values for the regressions and their residual plots (Fig. 7) were very similar. All variants that included central or total area as a variable had a better determination (in terms of R_a^2) than 0.83. A general feature was that the R_a^2-value for the untransformed power models lay lower ($\Delta > 0.02$) than the corresponding transformed models. A combined plot for $\lg(S_{tot}) = c + z \cdot \lg(A_{tot})$ and $S_{tot} = c \cdot A_{tot}^Z$ shows that the transformed model fits better to the smaller values (Fig. 8). Major differences occur first when one extrapolates the models to large areas, e.g. 22 km², the area of the Dalby district. The transformed power model predicts 2392 species, while the untransformed power model predicts 1142 and the logarithmic model 258. The number of species found in the district of Dalby (Dalby socken) was 604 (Almquist, 1965). None of the models comes close to the real value. Rydin & Borgegård (1988) who also found only small differences between the models found that the untransformed power model came very close to the actual number when they extrapolated to 100 km². All three models have considerably large maximal residuals of ≈25 species. The largest value is found in the
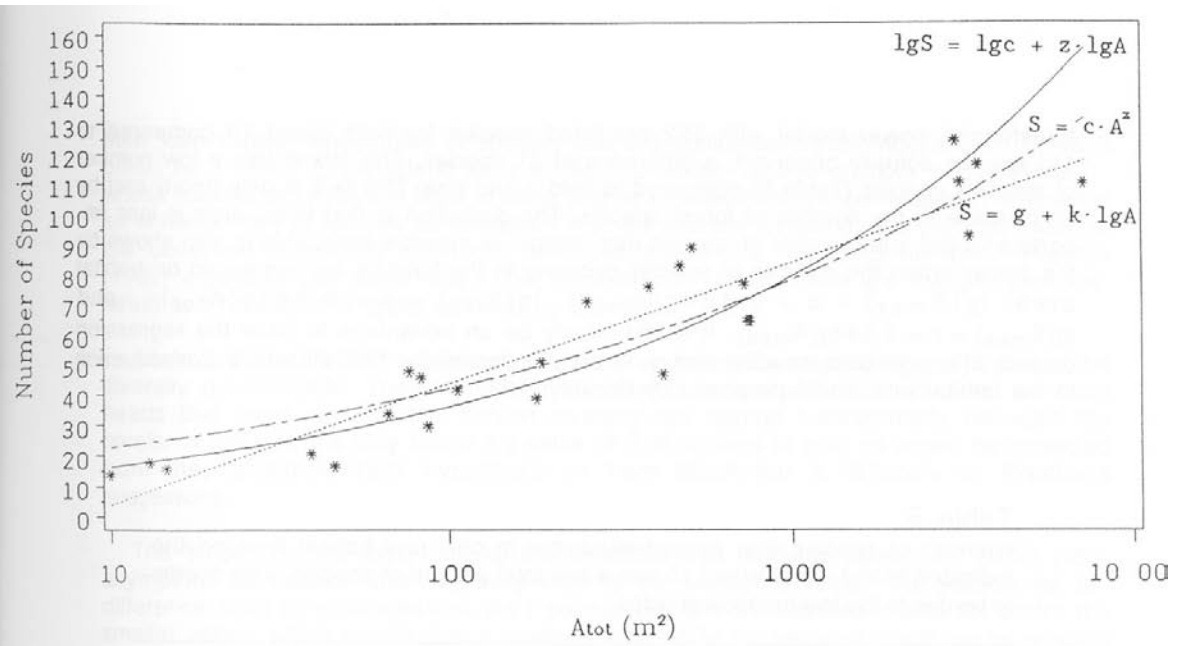
Fig. 8

Species–area curves generated by different statistical models: transformed power (—), untransformed power (–·–), and logarithmic (---). (∗)=observed numbers.
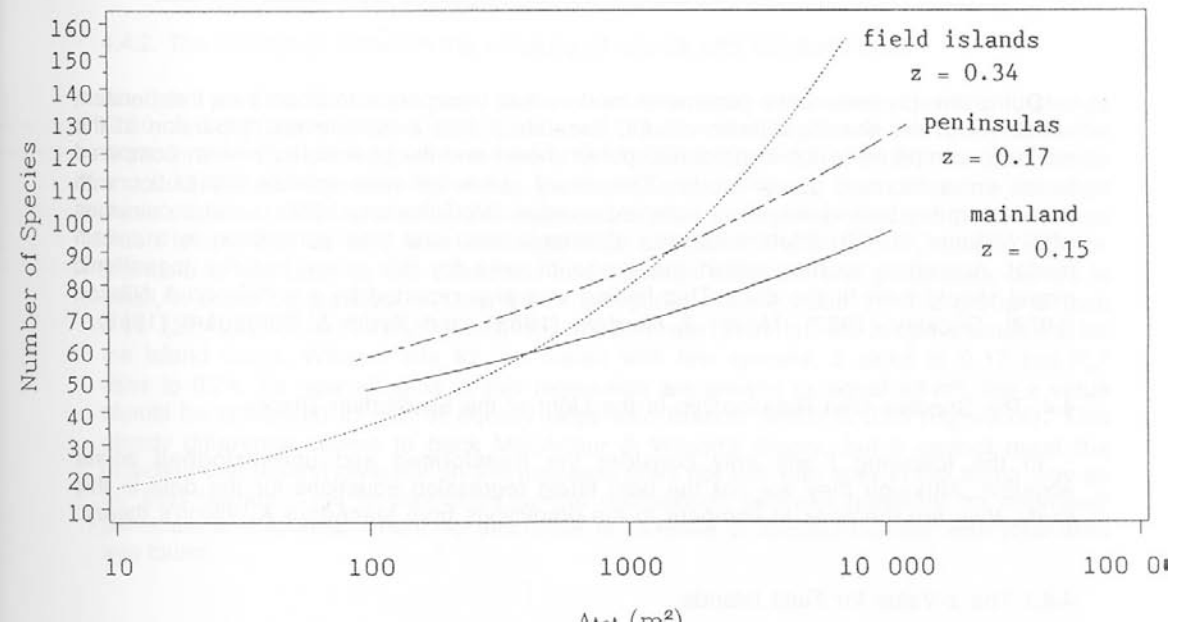

Fig. 9. Predicted species number for field islands (...), peninsulas (---), and mainland (—), by equation $(\lg(S_{tot})=c+z\cdot\lg(A_{tot}))$.

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transformed power model with 152 predicted species for field island 10 compared to 111 species actually observed, a difference of 41 species. This island has a low number of meadow species (Table 5) compared to field island size. This lack is only poorly met by an increase in the number of forest species. The deduction is that forest area is less important for the total number of species than margin or meadow area. This is also shown by the slopes when the number of species occuring in the habitats are regressed on habitat area: $\lg(S_{mar}) = c + 0.48 \cdot \lg(A_{mar})$, $\lg(S_{for}) = c + 0.24 \cdot \lg(A_{for})$, and $\lg(S_{mea}) = c + 0.34 \cdot \lg(A_{mea})$. It would clearly be an advantage to base the regression on area of margin plus meadow and on forest simultaneously. This will lead in consequence to the habitat unit model proposed by Buckley (1982).

Table 5.
Number of species that exclusively occur in only one habitat type on the indicated island. Field island 10 has a low total amount of species. This seems to be due to the few meadow species.

island nr.	total area [m^2]	number of plant species that grow only in			
		margin	forest	meadow	forest& meadow
2	3097	20	9	29	22
5	3005	29	2	20	20
10	7192	24	12	9	6
11	3314	14	5	17	8
49	3507	18	3	24	12

Out of the presented two-parameter models that incorporate total area as independent variable I prefer the logarithmic model, because it has a more even dispersion in the residuals compared to the transformed power model and the best fit (R_a^2) when compared to the untransformed power model. This infers rather an even species distribution with about as many individuals in all sampled species (McGuinness, 1984a), and it coincides with Williams' (1943) different classes of sample area and their connection to a certain model. According to him, within the range of area for this study just the logarithmic model should best fit the data. This finding was also reported by e.g. Nilsson & Nilsson (1978), Buckley (1982), Møller & Rørdam (1985), and Rydin & Borgegård (1988).

4.4. The Species-Area Relationship in the Light of the Equilibrium Theory

In the following I will only consider the transformed and untransformed power equation. Although they are not the best fitting regression equations for the data in this study, they are the ones to compare to the predictions from MacArthur & Wilson's theory.

4.4.1 The z-Value for Field Islands

The expected slope for the species-area curve on islands is in the ideal case 0.25 and between 0.15 and 0.39 for actual values (May, 1975, cited in Coleman, 1982). The corrected slope (Sprugel, 1983) from the regression equation (transformed power) for the field island data is 0.35, near to the upper limit. MacArthur and Wilson (1967, p.17)

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explain this with a growing heterogeneity of habitats on large islands. Each habitat then "can support ensembles of species that are ecologically semi-independent of each other. As a result ... the island as a whole is breaking up into multiple 'semi-islands' ... whose species can evolve at least to some degree as independent assemblages. The result is an enhancement of species accumulation that will account for some, and perhaps most, of the observed increment of insular z-values above the predicted number." Preston (1962) argues in the same way. The "semi-islands" in this case are margin, meadow, forest and boulder-rich spots covered by thin soil.

Abele & Patton (1976) published a report that makes the dependency of z on habitat diversity questionable. They were able to show in their study of crustaceans on coral heads that there was neither habitat diversity nor habitat heterogeneity between the corals. In spite of this they found a z-value of 0.35 instead of zero as would be expected from the habitat-diversity hypothesis or from MacArthur & Wilson's or Preston's suggestions.

The 'slope', i.e. the exponent, for the untransformed model is albeit 0.27 ±0.05 (95% asymptotic confidence interval), very near to the predicted value. The reason for the difference must be mathematical. As I pointed out, the transformed model fits better the smaller values which results into a steeper slope while the untransformed model predicts the high values better, the slope is consequently flatter.

This situation, to have two different z values produced by two variants of the same mathematical equation, makes it hard to compare the absolute z-values to MacArthur & Wilson's predictions, who did not specify the variant, and then to draw conclusions. This shows the importance of choosing a particular model and interpreting slope values cautiously.

4.4.2. The Difference Between the z-Values of Islands and Mainland Sites

Another prediction about the slope concerns the difference between islands ($0.20 < z < 0.39$) and mainland sites ($0.12 < z < 0.17$). For similar sites in the study area the slope in the transformed power model is 0.17 (SE=0.03, n=9, R_a^2=0.80) for peninsulas and 0.15 (SE=0.06, n=10, R_a^2=0.31) for the mainland (Fig. 9). The difference between these slopes is minimal. Mainland and peninsula slopes compared to island slope are thus much lower. But as only one mainland site is smaller than 100 m^2, as the R_a^2 for mainland is low, and as the difference in z between mainland and peninsula curves is small, it could be justified to lump these categories. The z value for this group is then 0.18 (SE=0.037, n=19, R_a^2=0.54), still much lower than for the slope calculated for the island curve. Without site 82, an outlier with few species, z sinks to 0.17 but R_a^2 rises to 0.74. As now all sites in this regression are greater or equal 88 m^2, the z value should be compared to that of equally large field islands, which is 0.25 (R_a^2=0.76). This steady difference seems to back MacArthur & Wilson's theory, but it cannot meet the objection that habitat diversity on the mainland does not rise with area in the same way as for field islands. This is supported by the comparison between quadrats on mainland/ peninsula and islands, where no difference in increase of species number with total area was found.

4.5. Evidence for the Habitat-Diversity Hypothesis

4.5.1. Random Placement ?

Since the equilibrium theory fails to explain the observed patterns in the species-area curve for field islands, there remain two testable alternatives: random placement and habitat-diversity. A test for deviation from patterns predicted by random placement can be carried out for the five smallest field islands by using the data from the quadrats. I

randomly picked quadrats from four equally large islands (no. 2, 5, 11, and 49) and lumped them to make up two of each 16 m^2, 32 m^2 and 48 m^2 quadrats. From these I constructed a double logarithmic species-area curve. This curve had a slope of 0.47 which differs a lot from 0.14, the slope for field islands smaller than 50 m^2 (i.e. no. 8, 19, 20, 23, and 60). This means that for these five field islands random placement is not very probable. Moreover the low values for the actually observed z does not agree with Coleman's et al. (1982) predicted value of $z>0.90$, which they calculated from a z-area relationship.

4.5.2. Habitat Diversity and Quality

In paragraph 4.3. I have already pointed out the individual role of habitats for the species-area curve. Now I will pick up the thread and show some more details. A glance at the correlation table shows that the three habitat variables, i.e. human influence, portion of boulder, and tree cover are significantly correlated to area:

The portion of boulder (BOULDER) usually decreases with increasing area (Fig. 10). Small field islands are those that consist of one large boulder, hidden for the biggest part in the ground and therefore not removed from the field. Large field islands exist because they consist of small but too many boulders or rocks to shovel them away. The latter ones have accumulated enough soil between them and on the stones, so that the percentage of 'naked' boulders is low and consequently meadow and forest vegetation is more prosperous.

Disturbance by human activities (INFLUENCE) is higher for small field islands because no farmer takes his time to deposit stones or material on the field island far away from the margin. Thus field islands with a high margin/central area ratio are more exposed to disturbance.

Tree cover on the meadow (TREECOVER)reflects mostly the presence of forest. Forest can be expected on a field island when, again, the ground consists of small boulders and rocks that have accumulated sufficient soil. For the investigated field islands there is a limit for the existence of single-boulder field islands: 126 m^2. This is consequently the lowest area limit for forests. Why this should be so and whether a limit is a general feature for field island forests must remain unexplained.

The habitat variables thus seem not only to describe habitat diversity but also habitat quality. This is a further evidence that habitat diversity plays the major role for the species-area relation.

4.5.3. The Best Regression Equation

The best regression model in terms of R_a^2 and residual plot appearance (Fig. 7d) is $lgS_{tot} = 1.3 + 0.24\ lg(A_{cen}) - 0.3\ BOULDER^2$. Non-linear regression has again a lower 'slope' and a lower R_a^2-value, but the 95% confidence intervals for 'slope' and 'intercept' contain the values from the transformed model. That central area and not total area gives best fit reflects (1) that in small field islands (<37 m^2 for circular and an increasing limit for rectangular or triangular areas) the margin area is larger than the central area, that (2) at the same time the small field islands consist of one large boulder with poor soil cover especially in the centre and consequently few species there, and that (3) on these field islands the number of species found only on the margin is never more than a dozen. The

difference between central and total area becomes negligible for large field islands (e.g. for no. 10, margin area is only 6% of the total area).
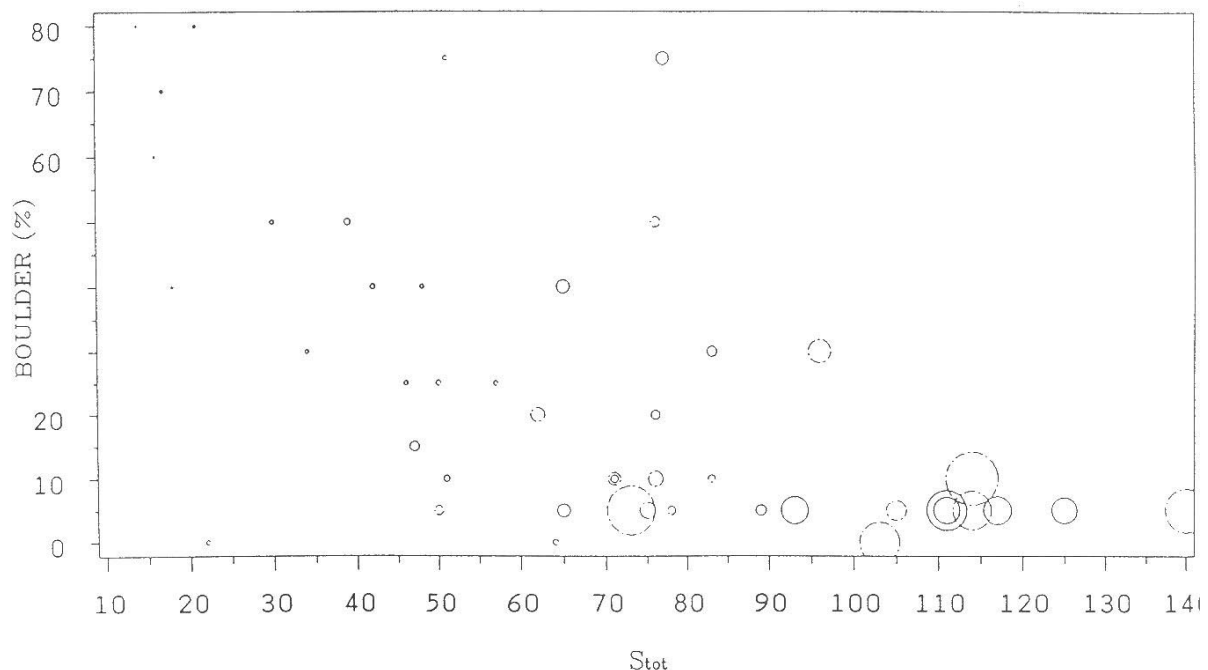

Fig. 10

Relation between sample area, portion of boulders and species number.
Circle area is proportional to island size, respectively sample area.
Field islands are indicated by a solid line.

The same reason holds for the entry of BOULDER^2 into the regression equation. The portion of boulder for the small field islands ranges from 0.4 to 0.8, which is when squared about the same size as the base 10 logarithm of area. So BOULDER is most important in the function for small field islands.

4.5.4. A Building Set for Field Islands

Finally a clear image arises about how species richness on the investigated field islands is controlled by habitat.

Small field islands consist of one large boulder and have more margin than centre. The central area has no or only very thin soil and therefore only sparse vegetation with few species, and the margin does not have more than a dozen additional species. As the area of field islands increases, the central part becomes more important, soil accumulates because the ground consists of several big boulders or a lot of smaller rocks. Thus the centre displays a richer vegetation, and the number of species that is found on the meadow and on the margin is about equal the number of species found only on the margin ($\approx$20). Still larger field islands have enough soil to support groups of trees. Their shading changes the environment and brings along a number of forest species. The meadow will also increase in species richness due to the better soil while the number of species that are confined to the margin still lies around 20. Thus the increase in area does not only

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increase habitat diversity but implies an ameliorated environment from the view of most higher plants.

5. ACKNOWLEDGEMENTS

6.1. Summary in Swedish - Sammanfattning

I Dalbytrakten, 12 km söder om Uppsala, undersökte jag artrikedomen för kärlväxter på 25 åkerholmar, som är mellan 10 m^2 och 7 ha stora. Utgående från Kellys et al. (1989) tillvägagångssätt, lade jag också ut provrutor (16 m^2) på varje holme och räknade arterna inom rutan. Enligt MacArthur & Wilsons jämvikts-teori (1967) borde det finnas ett samband mellan antal arter per 16m^2 yta och åkerholmens storlek, därför att det är sannolikare på större holmar än på mindre att arter som försvinnar från en viss yta ersätts av andra arter som lever i närheten. Två andra hypoteser, habitatdiversitets-hypotesen och slump-urvals hypotesen (random placement hypothesis) förutsäger att antal arter i en sådan provruta skulle vara oberoende av ö-arean.

För antalet arter på hela holmen är bästa modellen den logaritmiska ekvationen S=g+k·lg(A$_{tot}$), om man bara betraktar två-parameter-modeller. z-värdet (lutningen respektive exponenten) i de två geometriska modellerna S=c·A$_{tot}$^{z} och lg(S)= lg(c)+z·lg(A$_{tot}$) skilde sig anmärkningsvärd (0,27 och 0,35). Skillnaden är emellertid matematisk förklarbar. Genomsnittet för både z-värden kan anses överenstämmande med jämviktsteorin, men kan också förväntas enligt andra teorier.

En skillnad i lutningen mellan 'fastland' och åkerholmar som jämviktsteorin förutsäger, kunde visas, men kan förklaras av att habitatsdiversitet på fastlandet är mindre beroende av arean än den är på åkerholmar. Åtminstone för de fem minsta åkerholmarna är antalet arter troligtvis inte ett slumpmässigt urval av arter (random placement).

Något samband mellan antal arter per ruta och holmens storlek kunde dock inte påvisas. Detta tyder på att extinktionstakten är oberoende av åkerholmens storlek. Avståndet till fastlandet fanns inte heller har någon korrelation med artrikedomen. Därmed kan två av de grundläggande antagningar för jämviktsteorin inte styrkas.

Desutom är antal habitater och tre mätta habitatvariabler (andel hällyta, mänsklig inverkan och trädtäckningen på ängsdelen) beroende av åkerholmens yta och förekomsten av häll eller stenar. Mindre åkerholmar består av hällblock och har tunt jordtäcke, och artantalet är därför lågt. Större holmar ligger på blockig mark och har tillräcklig jord för att bära träd eller lundar tillsammans med en skuggtolerant flora, och artrikedomen är därför stor.

6.2. Summary in German - Zusammenfassung

In der Gegend von Dalby, 12 km südlich von Uppsala, Schweden, untersuchte ich die Art-Fläche-Beziehung für Gefäßpflanzen auf 25 Ackerholmen -leichte Erhebungen im Acker, die wegen ihres Reichtums an Steinen nicht bearbeitet werden. Die Größe der Holme erstreckt sich von 10 m^2 bis 0,7 ha. Nach einem Vorschlag von Kelly u.a. (1989) legte ich ebenfalls auf jedem Holm 16 m^2 große Probeflächen aus und zählte die vorhandenen Arten. Nach der Gleichgewichtstheorie von MacArthur & Wilson (1967) sollte die Artenmannigfaltigkeit der Probeflächen von der Größe des Ackerholmes abhängen, weil es auf größeren Holmen wahrscheinlicher ist, daß Arten, die von einer gewissen Fläche verschwinden, durch andere aus der näheren Umgebung ersetzt werden. Zwei andere

Hypothesen, die Habitatdiversitätshypothese und die Zufallsbesetzungshypothese (random placement), sagen voraus, daß die Anzahl der Arten von der Gesamtfläche unabhängig ist.

Für die Beziehung zwischen allen Arten des ganzen Ackerholms bot die logarithmische Gleichung $S_{tot}=g+k \cdot lg(A_{tot})$ die beste Ausgleichsgerade, wenn man nur Modelle mit zwei Parametern betrachtet. Die Steigung (z) für die beiden geometrischen Funktionen $S_{tot}=c \cdot A_{tot}^{z}$ und $lg(S_{tot})=lg(c)+z \cdot lg(A_{tot})$ unterschieden sich beachtlich (0,27 und 0,35). Der Unterschied läßt sich jedoch mathematisch erklären. Der mittlere z-Wert stimmt mit der Gleichgewichtstheorie überein, wird aber auch von anderen Theorien erwartet.

Ein Unterschied in der Steigung zwischen 'Festland' und Ackerholmen, wie er nach der Gleichgewichtstheorie zu erwarten ist, trat jedoch auf, könnte aber darauf zurückzuführen sein, daß auf dem Festland die Habitatdiversität nicht in gleicher Weise von der Fläche abhängt wie auf Holmen. Zumindest für die fünf kleinsten Holme ist die Artenzahl wohl nicht durch zufällige Besetzung (random placement) bestimmt.

Einen Zusammenhang zwischen Artenzahl je Probefläche und Gesamtfläche konnte ich in dieser Untersuchung aber nicht finden. Das bedeutet, daß die Aussterberate für Holme unabhängig von deren Größe ist. Auch die Entfernung der Ackerholme vom 'Festland' war nicht mit der Anzahl der Arten auf den Holmen korreliert. Damit sind zwei der grundlegenden Annahmen der Gleichgewichtstheorie verletzt.

Ansonsten ist die Anzahl der Habitate und drei gemessene Habitatvariablen (Steinanteil, menschlicher Einfluß und Deckungsgrad der Baumschicht auf der Wiese) abhängig von der Größe des Ackerholmes. Kleine Ackerholme bestehen aus einer großen Felsenfläche mit einer dünnen Bodenschicht, deshalb wachsen darauf nur wenige Arten. Große Ackerholme befinden sich dort, wo der Boden zu viele klobige Steine hat, um ihn zu beackern, sie haben aber ausreichend Erde, um Bäume und Wäldchen zu tragen; der Artenreichtum ist daher groß.

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Appendix 1

1. Variables used in original correlation matrix

Pearson correlation coefficients were calculated in a matrix between the following variables:

S_{tot}, S_{cen}, S_{mar}, S_{for}, S_{mea},
$lg(S_{tot})$, $lg(S_{cen})$, $lg(S_{mar})$, $lg(S_{for})$, $lg(S_{mea})$,
$lg(A_{tot})$, $lgA(_{cen})$, $lg(A_{mar})$, $lg(A_{for})$, $lg(A_{mea})$,
INFLUENCE, TREE-COVER, BOULDER,
A_{for}/A_{mea}, A_{mea}/A_{tot}, A_{mar}/A_{tot}, A_{for}/A_{tot},
DISTfor, DISTmea, DISTmin,
QU_ALL,

2. Chart about the variables used in statistical evaluation

independent variables	dependent variable										
	S_{tot}	S_{cen}	S_{mar}	S_{for}	S_{mea}	$lg(S_{tot})$	$lg(S_{cen})$	$lg(S_{mar})$	$lg(S_{for})$	$lg(S_{mea})$	$1/S_{tot}$
A_{tot}	N										N
A_{cen}	N										
$1/A_{tot}$	S					S					S
$1/A_{cen}$	S					S					S
$lg(A_{tot})$	MS	S				MS	S				S
$lg(A_{cen})$	MS	S				MS	S				S
$lg(A_{mar})$			G					G			
$lg(A_{for})$	S			G		S			G		S
$lg(A_{mea})$	MS	S			G	MS	S			G	S
$2lg(A_{tot})$	S	S				S	S				S
$lg(A_{tot})\,lg(A_{cen})$	S	S				S	S				S
$2lg(A_{cen})$	S	S				S	S				S
BOULDER	MNS	S				MS	S				S
BOULDER^2	NS	S				MS	S				S
BOULDER-0.3	S					S					S
SIGN(BOULDER-0.3)	S					S					S
1-BOULDER	S					S					S
1-BOULDER^2	S					S					S
1/BOULDER	S					S					S
TREECOVER	MS	S				MS	S				S
TREECOVER^2	S	S				S					S
1/TREECOVER	S					S					S
INFLUENCE	MS	S				MS	S				S
INFLUENCE^2	S	S				S					S
1/INFLUENCE	S					S					S
SIGN(A_{cen})	S					S					S
A_{mar}/A_{tot}	MS	S				MS	S				S
A_{mea}/A_{tot}	MS	S				MS	S				S
A_{for}/A_{tot}	MS	S				MS	S				S
A_{for}/A_{mea}	MS	S				MS	S				S
DISTfor	S	S				S	S				S
DISTmea	S	S				S	S				S
DISTmin	S	S				S	S				S
QU_ALL	MS					S					

Abreviations: G: General Linear Model regression (GLM), M: Maximum R-Square Improvement method for Stepwise Regression (includes GLM), N: Non-linear Regression, S: Stepwise Regression (includes GLM)