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Fern species diversity in relation to spatial scale and structure

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Abstract

Species with different requirements can coexist if the environment varies in space; we therefore expect a positive relationship between species diversity and environmental heterogeneity. In this thesis I examine the influence of environmental structure on patterns of fern diversity in one hectare of old-growth forest and compare these patterns to other surveys covering a broad range of scales. The nineteen species recorded in the hectare had non-random spatial distributions and differed in their soil preferences. Diversity was positively related to soil moisture and negatively related to soil fertility, but there was no relationship with environmental variance. The counteracting influence of dispersal may predominate over selection processes at the hectare scale. Both species-area curves and the decreasing correlation of species composition with distance had very similar slopes over quadrat sizes ranging from 1 x 1 m to 50 x 50 km, suggesting that some diversity patterns may be independent of scale.

Résumé

Un environnement qui varie dans l'espace facilite la coexistence de plusieurs espèces; on s'attend donc à observer une relation positive entre la diversité des espèces et l'hétérogénéité de l'environnement. Cette thèse traite d'une étude de la structure environnementale et son influence sur la diversité des fougères à l'intérieur d'un hectare de forêt. Par la suite, je compare les résultats de cette première analyse à d'autres études effectuées à différentes échelles spatiales. Les dix-neuf espèces retrouvées dans cet hectare possèdent des distributions non-aléatoires ainsi que des préférences distinctes quant aux conditions du sol. On observe une relation positive entre la diversité et l'humidité du sol, une relation négative entre la diversité et la fertilité du sol, mais aucune relation avec la variation de l'environnement. L'immigration et la dispersion des organismes s'opposent à l'action de la sélection naturelle en favorisant une répartition plus aléatoire entre les sites; ces effets pourraient prédominer à l'échelle locale de cette étude. La relation entre la diversité et l'aire d'un site, ainsi que la relation entre la composition spécifique et la distance entre deux sites, possèdent des pentes très semblables sur une gamme d'échelle allant de quadrats de 1 m x 1 m jusqu'à 50 x 50 km. Ces résultats suggèrent que certaines répartitions spatiales de la diversité sont indépendants de l'échelle spatiale.

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Preface

The following text has been reproduced here in accordance with the *Guidelines for Thesis Preparation* of the Faculty of Graduate Studies and Research:

“Candidates have the option of including, as part of the thesis, the text of one or more papers submitted or to be submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must be bound as an integral part of the thesis.

If this option is chosen, **connecting texts that provide logical bridges between the different papers are mandatory**. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

The thesis must still conform to all other requirements of the “Guidelines for Thesis Preparation”. **The thesis must include:** A Table of Contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a review of the literature, a final conclusion and summary, and a thorough bibliography or reference list.

Additional material must be provided where appropriate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, **the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent**. Supervisors must attest to the accuracy of such statements at the doctoral oral defence. Since the task of examiners is made more difficult in these cases, it is in the candidate’s interest to make perfectly clear the responsibilities of all the authors of the co-authored papers.”

The two chapters of this thesis have been written in manuscript style and are co-authored by myself, Professor Graham Bell and Torsten Bernhardt. Both chapters have been submitted to the peer-reviewed journal *Ecography*. Torsten Bernhardt and I performed the field and lab work for Chapter 1, and worked together to write computer programs for the analyses. I collected and analyzed the literature data for Chapter 2, performed the analyses for both chapters, and wrote the manuscripts. Professor Bell provided guidance and suggestions at all stages of the project and edited the manuscripts.

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General Introduction

The distribution of individual organisms forms a complex mosaic in which ecologists observe patches, gradients, and hotspots of diversity. Difficulties in describing and quantifying this complexity have resulted in a proliferation of esoteric indices and techniques (reviewed in Magurran 1988). The explanation of diversity poses an even greater challenge: so many hypotheses exist that it sometimes seems the study of diversity has been supremely unsuccessful (Palmer 1994). Starting from basic principles, the very existence of diversity is something of a paradox (Hutchinson 1961). One of the first lessons learned in introductory ecology and evolution classes is that in a mixture the single type, allele or species, which is fitter, faster, better and most prolific will increase in frequency until it has driven all others to extinction (Gause 1937). Most hypotheses to explain diversity gradients can be viewed as violations of this competitive exclusion principle (Palmer 1994). Disturbance by predators, disease, or physical forces such as ice storms or fire will tend to interrupt the gradual increase in frequency of the strongest competitor (Connell 1978, Huston 1979). Physical barriers between species may prevent them from interacting and may thus provide refuge for inferior competitors (Levin 1974). The immigration of individuals from outside areas can continually replenish the ranks of a dwindling species (Shmida and Wilson 1985). However, the most common promoter of species coexistence may well be variation of the environment, either spatial or temporal, which allows species with different requirements to coexist (Palmer 1994). The study of spatial diversity patterns involves consideration of three important and interrelated issues: area, environmental heterogeneity, and scale.

The species-area curve is the oldest and probably the best-known diversity pattern (Rosenzweig 1995). We know that area plays a dominant role in regulating diversity, since the number of species increases with area at every scale larger than individual organisms (Rosenzweig 1995). An understanding of how and why diversity increases with area provides insight into the evolutionary and ecological processes which structure communities. On a practical level, species-area curves are used by conservation biologists to predict the loss of species expected from a given decrease in habitat area (e.g. Pimm et

al. 1995). Consequently, a thorough understanding of the form and properties of species-area curves remains central to ecology. As discrete and tractable samples of area, islands played an important role in the development of a coherent theory for species-area curves (MacArthur and Wilson 1967). The number of species on an island represents a balance between immigration and extinction: fewer species will immigrate to distant islands, and more species can coexist in larger areas. The mechanisms controlling diversity are essentially similar for mainland sites, although immigration will tend to exert a stronger influence (Rosenzweig 1995). The two main explanations for why more species persist in larger areas are the area *per se* hypothesis and the habitat diversity hypothesis (Connor and McCoy 1979). According to the former, larger areas can support more individual organisms, such that population sizes are larger and more species resist extinction even if the environment is homogeneous (Rosenzweig 1995). In contrast, the habitat heterogeneity hypothesis states that more different kinds of habitat occur in a larger area, permitting the coexistence of species with different requirements (Williams 1964). Several studies have shown a relationship between the number of habitats in an area and species diversity (e.g. Anderson 1978, Boecklen 1986, Haila 1983) but others have observed an effect of area with no additional contribution from habitat diversity (e.g. Simberloff 1976, Martin 1981, Nilsson et al. 1988). The main problem with such studies is that the "habitat" is a subjective and artificial construct. In reality, different habitats grade into one another without any well-defined boundaries, and each location comprises a continuum of many varying environmental conditions such as moisture, temperature, soil type, etc.

To reduce subjectivity, the habitat diversity hypothesis can be reformulated in the following way: "areas with more environmental variation should support a greater number of species". Empirical evidence for this hypothesis can be collected in a systematic, quantitative way by relating diversity patterns to precise and repeatable measures of environmental heterogeneity. Detailed examinations of soil characteristics have revealed that substantial environmental variation exists at scales of centimetres to hundreds of metres (Robertson et al. 1988, Palmer 1990, Lechowicz and Bell 1991), while the variance of other environmental features continues to increase with distance

over hundreds of kilometres (Bell et al. 1993). If plant species exhibit distinct environmental preferences and have different relative fitness levels under different combinations of environmental conditions, then we expect to observe a positive relationship between species diversity and well-defined measures of environmental heterogeneity.

The effect of spatial scale, or the resolution and total extent of observations or measurements, is essential to consider in any ecological study. Many natural patterns and processes are fractal and are characterized by varying degrees of self-similarity across scales (Williamson and Lawton 1991, Palmer 1988). Note that in ecology, scale generally has the opposite meaning of that employed by geographers, who refer to a very detailed map of a small area as a large scale, whereas a map of a continent is considered small-scale. Diversity patterns are often studied at either very small scales (community ecology) or at very large scales (biogeography); comparatively few studies deal with intermediate scales which are sometimes referred to as “regional” or “landscape” scales (e.g. Böhning-Gaese 1997). As noted previously for habitats, there are in reality no distinct or characteristic scales but instead a continuous gradient from small to large. Ecologists now recognize the importance of considering the effects of scale and how the relative importance of different processes which affect species distributions changes with scale (Ricklefs 1987, Auerbach and Shmida 1987, Cornell and Lawton 1992). At local scales, interactions among plants and dispersal limitations will strongly influence distribution patterns, while differences in annual rainfall and minimum winter temperatures may be more important at very large scales. The change in relative importance of different factors with scale may help to explain the existence of so many different hypotheses about diversity gradients.

One of the ongoing research programs in the Department of Biology at McGill University seeks to describe and understand the relationships between environmental structure and the diversity of populations and species (essentially the same question addressed at a different taxonomic scale) (Bell and Lechowicz 1991, Lechowicz and Bell 1991, Bell et al. 1991, Bell et al. *subm.*). We are fortunate to have an excellent study site

for these investigations in the Mont St. Hilaire Nature Reserve. This ca. 1200 ha site is a hill formed by an intrusion of volcanic rock which rises 300 m above the St. Lawrence valley. The old-growth forest ecosystem there has never been significantly cut or otherwise disturbed. Several studies have described the spatial structure of environmental variance and its relationship to the growth, distribution and diversity of taxa such as trees, ferns, and the sedges of the genus *Carex*. This thesis fits into the broader research program by examining patterns of spatial variation in relation to scale and structure, and relationships between species diversity and environmental heterogeneity.

The first chapter of this thesis is concerned with the distribution patterns of fern species and environmental variation within one hectare of undisturbed forest. From a meter-level survey of the plot, I describe the spatial arrangement of fern species and the structure of environmental variance, and investigate relationships between diversity and the environment. Bell and Bernhardt (in prep.) have observed that the variance of slope, solar radiation and water flow within 1 ha quadrats explains a substantial portion of the variation in fern species diversity, equivalent to the amount explained by the mean conditions of growth. I examine whether similar relationships can be observed at scales smaller than 1 ha by measuring soil properties relevant to plant growth and dispersal.

The second chapter of this thesis uses a comparative approach to examine spatial patterns of fern diversity across a range of scale, from our very intensive local field survey to the distribution of the European flora. Species-area curves and the spatial structure of diversity patterns are compared to null models of random distribution at each scale. I examine whether species diversity patterns exhibit scale-independence and evaluate the relative contribution of spatial scale and structure to these patterns.

Biodiversity is both endlessly fascinating and vitally important. The type of systematic biological survey presented in this thesis provides a useful summary of variation among sites and among species. It is hoped that more studies of this type will be conducted using consistent effort for each site as well as detailed measurements of physical variables. This data can then serve for comparisons among different taxa,

systems and scales, in order to achieve more rigorous testing of ecological and evolutionary hypotheses. A better understanding of the spatial structure of diversity should also be helpful in the prediction of diversity levels in relatively poorly-studied regions (Colwell and Coddington 1994). Armed with more complete knowledge and understanding, we may perhaps improve our chances of conserving biodiversity.

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Chapter 1

Environmental heterogeneity and the spatial structure of fern species diversity in one hectare of old-growth forest

Abstract

The precise relationship between species diversity and spatial heterogeneity has not often been investigated using quantitative and repeatable measures of environmental variation. In this study, we map the meter-level distribution of fern species in one hectare of old-growth forest and test for a relationship between diversity and heterogeneity of physical features and soil conditions. The nineteen species recorded in the hectare were non-randomly distributed and varied greatly in abundance and spatial aggregation. Different species distributions were not independent of one another; three groups of species were identified which occurred together significantly more often than random expectation. Physical and soil conditions were highly variable and spatially autocorrelated from the 5 m scale up to the extent of the whole hectare. Based on the sites where they grew, species differed in their preferences for soil moisture, fertility and pH. Fern diversity was highest at sites with high soil moisture and low soil fertility; however, there was no relationship between diversity and the environmental variance within quadrats. Unpredictable spatial distribution patterns produced by processes of dispersal and immigration may obscure any relationship between diversity and spatial heterogeneity at the scale of this survey.

Introduction

A number of ecologically equivalent species can exist in the same place if environmental heterogeneity prevents one competitive species from excluding all others (Crawley 1986, Palmer 1994). For this reason, variation in habitat diversity has been proposed as an explanation for many diversity gradients and patterns, including the species-area curve (Williams 1964), the latitudinal diversity gradient (Pianka 1966) and the hump-shaped relationship between diversity and productivity (Tilman 1982). Many studies have described a relationship between species diversity and the number of habitats in an area (e.g. Harman 1972, Anderson 1978, Boecklen 1986), yet others have found no effect of habitat diversity once the correlated effect of area was removed (e.g. Simberloff 1976, Martin 1981, Nilsson et al. 1988). One flaw of such studies is that the "habitat" is a subjective, simplified categorization of environmental conditions. This is useful and quite convenient when comparing sites as different as a meadow and a pond, but environments are not homogeneous even at very small scales (Robertson et al. 1988, Palmer 1990, Lechowicz and Bell 1991) and heterogeneity continues to increase even at very large scales (Bell et al. 1993). There are rarely precise boundaries between distinctive habitats or communities but instead a continuous gradation of environmental conditions or species composition, which may or may not be perceived depending on the scale of observation (Palmer and White 1994a). Therefore, we require straightforward and quantitative measurements of environmental variance in order to establish a firm empirical foundation for the relationship between spatial heterogeneity and diversity. Variation of the environment may be studied with multiple, spatially-referenced measures of environmental conditions (e.g. Lechowicz and Bell 1991), or ideally with implant trials which provide a measure of environmental suitability from a plant's perspective (e.g. Schoen et al. 1994, Bell et al. *subm. a*).

Bell and Bernhardt (in prep.) have analyzed the diversity patterns of a community of 38 species of ferns after a survey of 1016 one-hectare quadrats conducted in undisturbed old-growth forest. Species richness was greatest in hectares characterized by high soil moisture, low solar radiation and low slope; together these three variables

accounted for 22% of the variance of diversity among hectares. Species diversity was also positively related to environmental variance independently of the effect of the average conditions of growth, and progressively more variation was explained by environmental heterogeneity as scale was increased by aggregating hectares into larger units. At the scale of 25 ha, within-quadrat environmental variance explained 25% of the variance in species richness, an amount equivalent to that explained by the mean environmental conditions.

In this study we examine the effects of environmental variance on fern diversity at scales smaller than one hectare. Diversity patterns change according to the scale of observation (Palmer and White 1994b), as does the relative importance of different factors which influence diversity (Auerbach and Shmida 1987). Biotic interactions among plants are more likely to be important at small scales, while physical factors may play a greater role in distribution patterns at larger scales (Reed et al. 1993). We conducted a biological survey of one hectare of old-growth forest, recording the distribution of ferns in every square metre. The fine resolution of the study approaches the scale of individual plants, allowing a detailed exploration of the spatial structure of species distribution patterns. In the following analyses, we examine the variance of diversity among sites, the change in species composition with distance between sites, the spatial structure of soil conditions and the differences among species in their abundance, dispersion and environmental preferences. Finally, we test whether diversity increases with environmental variance within the hectare.

Methods

Biological survey

The study plot was located at Mont St. Hilaire, Quebec, a UNESCO Man and the Biosphere Reserve. The “mountain” is an isolated hill formed of intrusive igneous rock which rises 300 m above the surrounding St. Lawrence valley and is covered in mature

forest dominated by beech and sugar maple. It is the northernmost remnant of old-growth mixed deciduous forest in eastern North America and has never been substantially cut or disturbed. One hectare of forest has been mapped and surveyed for tree diversity as part of the Smithsonian Institution - Man and the Biosphere program. The terrain of this hectare plot varies from a low, flooded area in the south-west corner to a steep, rocky slope in the opposite corner. The hectare was delineated by surveyors who installed a grid of permanent pins in the soil at 10 m intervals. During July and August 1997, we used these 10 m markers to survey the hectare for ferns. We installed six ropes around the sides and across the center of each 10 m square and used markings on the ropes and metre sticks to delimit each individual square metre. The 10 m markers were set out from an aerial view of the hectare, and consequently some 10 m squares which lay on a steep slope actually measured 11 or 12 m on a side. We surveyed each metre on the ground, producing a slightly irregular grid consisting of 10 926 quadrats rather than 10 000. In each square metre, we recorded the number of stems of each species of fern. Individual plants were defined as distinct crowns or clusters of fronds emerging from a single point. However, several species grew in dense clumps in which the boundaries between plants were not easily discernible, and in the case of *Cystopteris bulbifera* clonal groups are clearly formed by asexual propagation through bulblets. The number of stems may not, therefore, represent an equivalent number of individual plants.

Measurement of environmental heterogeneity

We recorded the amount of cover of different features in each square metre including rock, fallen wood, stumps, paths, tip-up mounds, mud (waterlogged soil) and water (small streams and pools) in increments of 10% between 0 and 100 %; ground area not classified in one of these categories was covered by leaf litter. The strong topographic gradient of the hectare can be visualised by the distribution of these variables (Fig. 1). The steeply sloping north-east corner has a high proportion of rock, whereas path, mud, and water occur only in the flat south-west corner. Wood, stumps and tip-up mounds (not shown on map) were rather evenly scattered throughout the hectare, with most fallen trees pointing downslope on the steep incline. The amount of fallen wood is likely to vary

Figure 1. Physical features within the study hectare: rock (circles), path (squares), mud (crosses), water (triangles). The variation in colour intensity from white to black indicates 0 - 100 % cover of each square meter.



0 20 Meters



considerably through time; a very severe ice storm in January 1998 has substantially increased the amount of fallen wood since our survey. Elevation was recorded at 20 m intervals within the hectare but was not used in analyses because the resolution was not fine enough to detect the small-scale topographical gradients which we observed in the field.

Soil samples were collected every 5 m within the hectare, one in each quadrant of each 10 m square on 2nd October, 1997. Loose litter was cleared from the surface of the site and the top 5 cm of soil were collected using 3 cm diameter cylindrical corers, stored in plastic film canisters and kept frozen until analysis. In the lab, the samples were thawed and weighed immediately, then air-dried for 3 days and reweighed to measure soil moisture content. Soilwater extracts were prepared by combining 2.5 g of soil from each sample with 100 ml of distilled water in a 250 ml Erlenmeyer flask. The mixture was left at room temperature for 24 hours, then filtered under vacuum through #1 Whatman filter paper and transferred into capped glass culture tubes and stored in the refrigerator. Twenty ml of this solution was used to measure pH, using a Fisher Accumet pH meter, Model 950. The remaining soilwater was used for a bioassay of soil quality using the growth of a green alga (*Chlamydomonas reinhardtii*) as an indicator of fertility. In successive experiments, two strains of *C. reinhardtii* (cc-1010 and cc-2938) were inoculated into tubes filled with 20 ml of soilwater, for a total of 400 tubes per strain; another series of 400 tubes were not inoculated and served as controls. The soilwater medium was not autoclaved before the assay, in order to preserve the original chemical composition of the medium. The cultures were grown in light cabinets, and culture density was measured on days 5, 10 and 15 after inoculation with a spectrophotometer. Over the course of the experiment, about 10 % of the control tubes showed some growth of wild algae with filamentous or sheet-like growth forms. No multicellular algal growth was observed in the corresponding treatment tubes which contained *Chlamydomonas*. However, due to the increase in density of the control tubes over time, we used only the first measurement from the control tubes as the initial density. The maximal density observed in the inoculated tubes, after subtraction of the control density value, constitutes our measure of soil fertility. We used the average density of the two strains, because the

environmental correlation was very high ($r = 0.84$); in other words, the strains had very similar responses to the different environments.

The frequency distribution of soil moisture was somewhat right-skewed; normality was not improved by any simple transformation, however, so untransformed values were used for analyses. Soil fertility values were similarly right-skewed and left untransformed. The frequency distribution of pH was highly left-skewed; a substantial improvement was obtained using the transformation: $x' = e^x$. To express the spatial structure of the environment, we examined the average variance of environmental conditions as a function of the distance between sites (Bell et al. 1993). The variance of the two environmental measurements for each pair-wise combination of sites were used to calculate average variance values within each distance class. The slopes of variance plots with logarithmic axes can be compared among variables, with a steeper slope indicating a more coarse-grained landscape.

Species diversity patterns

We compare the observed diversity patterns with those expected from a null model of random distribution of species among sites. The null model was created by allocating species randomly to sites in the data matrix, such that each species maintains its observed number of occurrences. We also examine the effect of scale on diversity patterns by aggregating the original 1 m² quadrats to form larger units, up to 25 x 25 m. These aggregate quadrats were used to construct a species-area curve for the hectare by plotting the average of all non-overlapping quadrats of each size; this approach is equivalent to taking the average of several nested species-area curves (Condit et al. 1996).

To express the degree of spatial dispersion of each species we use a generalized Poisson model, which provides a measure of aggregation based on the proportion of quadrats occupied by a species as scale is increased (Bell et al. *subm. b*). Dispersion is calculated based on the following formula:

$$m_L = 1 - u_L = e^{-m_1(1+c(L-1))}$$

where L denotes the area of the quadrats, m_L is the frequency of occupied quadrats at a given size L (the number of occupied quadrats divided by the total number of quadrats), u_L is the frequency of unoccupied quadrats, and c is a coefficient which represents the degree to which the distribution deviates from a random dispersion. The quantity m_1 is the number of quadrats occupied at the smallest scale of 1 m^2 quadrats. As quadrat size increases, the proportion of occupied quadrats, m_L , also increases and u_L decreases. For example, a randomly-distributed species that occupied 30/100 quadrats at the 1 m^2 size should occupy close to 30/50 quadrats if quadrat area is doubled to 2 m^2 . More generally, the frequency of unoccupied quadrats will decrease following $u_L = e^{-Lm_1}$ as quadrat size L is increased, for a random distribution. The frequency of unoccupied quadrats will also decline, but more slowly, for a species occurring in patches. By aggregating quadrats into larger units and observing the frequency of occupied sites at each scale, we can estimate c , because:

$$(1/u_L) du_L/dL = -c m_1$$

Therefore, $-c m_1$ is the slope of the regression of $\log u_L$ on L , and c can be calculated based on the observed slope and m_1 , the number of occupied quadrats at the 1 m^2 scale. A randomly distributed species has $c = 1$, with values less than unity indicating aggregation.

Species may have spatially aggregated distributions but remain independent of the distribution of other species. To explore the patterns of species co-occurrence, we examined the variance of species richness among quadrats as well as pair-wise comparisons of species coincidence. High variance in species richness among quadrats implies that there are "hotspots" of diversity where species congregate as well as other sites which are avoided by most species (Palmer and van der Maarel 1995), whereas low variance in species richness is taken as evidence for niche limitation (Wilson et al. 1987). We compared the observed variance of species richness to the null model expectation

based on the average variance from 100 randomisations of species distributions. We also calculated the expected variance of species richness assuming that species are distributed independently (but not necessarily randomly) as $V_e = \sum p_i(1-p_i)$, where p_i = the number of occurrences of species i divided by the total number of sites (Schluter 1984, Palmer and van der Maarel 1995). In order to identify positive or negative associations among species, we constructed a species by species matrix containing the number of 5 m quadrats in which each species occurred with one another. The original data matrix was randomised 10 000 times to obtain the mean number of pair-wise combinations expected by chance. Deviations from the expected mean were expressed in units of standard deviation and used as similarity measures for a cluster analysis to classify species into groups. Six available clustering algorithms in the SYSTAT analysis package were compared, including single, complete, average, centroid and median linkage and Ward's minimum variance method. The species by species analysis of associations was conducted using only the 10 most common species (those occurring in at least 20/400 sites) so that mean expected values would be sufficiently large.

The spatial structure of species distributions can be expressed by distance decay, or the change in species composition as the distance between sites increases. A correlation of species composition between each pair of quadrats was calculated as the binary covariance of the presence and absence of all 19 species, divided by the product of the standard deviation of the two sites (Richard et al. *subm.*). The average correlation was plotted for all points within distance intervals up to half the maximum distance, so that all sites contribute to each distance interval. We expect the correlation to decrease with distance if nearby sites tend to be similar while distant sites have different species compositions. A related analysis calculates the average species richness of pairs of quadrats as distance increases; diversity should increase with distance if the specific correlation decreases.

Species-environment relationships

The mean and variance of soil conditions for all 5 m quadrats where a species was found were used as measures of environmental preference (mean) and breadth of tolerance (variance). The variances of soil moisture (σ_{ms}^2), fertility (σ_{fy}^2) and pH (σ_{pH}^2) were combined into a general measure of environmental tolerance for each species as the geometric mean:

$$\sigma_E = (\sigma_{ms} \sigma_{fy} \sigma_{pH})^{1/3}$$

We estimated effects of the mean and variance of environmental variables on diversity through multiple linear regression. The number of species per quadrat was regressed on the mean values of physical variables (rock, wood, stump, path, tip-up mound, water) and of soil conditions (moisture, pH, fertility). The residuals of species richness from these regressions were tested against the residuals of the regressions between the mean and variance of each variable, in order to separate the effects of mean and variance. Spatial structure in the data implies that samples are not independent and significance values must be interpreted cautiously (Legendre and Fortin 1987); keeping this in mind we present the variables which contributed most strongly to explaining variation in diversity. These analyses were repeated at the 5, 10, 15, 20 and 25 m scales, with three different data sets at each scale created by shifting the origin of the grid to a different position when aggregating quadrats. There is no measure of variance for soil conditions at the 5 m scale since each quadrat is represented by a single measurement.

Results

Species distribution patterns

Nineteen species of ferns were recorded in the one hectare plot (Table 1). This site appears to be exceptionally diverse. A mountain-wide survey of 1016 hectares conducted

Table 1. Abundance and dispersion of the nineteen fern species recorded in the hectare. R is the number of 1 m² quadrats occupied by each species; r is the number of stems; r/R is the average number of stems per square metre, used to classify species according to habit as either rhizomatous (forming dense clumps through vegetative spread) (R) or caespitose (consisting primarily of distinct plants) (C); *c* is a coefficient which expresses the degree of dispersion with lower values indicating a greater degree of aggregation.

Species		R	r	r/R	habit	<i>c</i>
<i>Adiantum pedatum</i> L.	APE	1231	12364	10.0	R	0.009
<i>Athyrium filix-femina</i> (L.) Roth	AFF	892	2542	2.8	C	0.012
<i>Botrychium virginianum</i> (L.) Sw.	BOT	40	82	2.1	C	0.161
<i>Cystopteris bulbifera</i> (L.) Bernh.	CBU	923	13256	14.4	R	0.007
<i>Cystopteris fragilis</i> (L.) Bernh.	CFR	28	52	1.9	C	0.058
<i>Dennstedtia punctilobula</i> (Michx.) Moore	DPU	2	3	1.5	C	-
<i>Deparia acrostichoides</i> (Sw.) Kato	DAC	82	436	5.3	R	0.025
<i>Dryopteris carthusiana</i> (Vill.) Fuchs	DCA	100	139	1.4	C	0.083
<i>Dryopteris intermedia</i> (Muhl.) Gray	DIN	125	170	1.4	C	0.169
<i>Dryopteris marginalis</i> (L.) Gray	DMA	1223	1782	1.5	C	0.015
<i>Gymnocarpium dryopteris</i> (L.) Newm.	GDR	81	798	9.9	R	0.020
<i>Matteucia struthiopteris</i> (L.) Todaro	MST	39	63	1.6	C	0.054
<i>Onoclea sensibilis</i> L.	OSE	45	184	4.1	R	0.032
<i>Osmunda cinnamomea</i> L.	OCI	117	217	1.9	C	0.009
<i>Phegopteris connectilis</i> (Michx.) Watt	PCO	11	77	7.0	R	0.140
<i>Polystichum acrostichoides</i> (Michx.) Schott	PAC	87	157	1.8	C	0.101
<i>Polypodium virginianum</i> L.	PVI	1	17	17.0	R	-
<i>Pteridium aquilinum</i> (L.) Kuhn	PAQ	20	27	1.4	C	0.043
unidentified hybrid		6	19	3.2	C	0.080

in 1996 recorded a total of 38 species, with an average of 6.3 fern species per hectare, and a range of 0 to 18 (Bell and Bernhardt, in prep.). In other temperate regions, an area of 2.6 ha of secondary forest in the Duke Forest, North Carolina contained only 5 species of ferns (M. Palmer, pers. comm.). More comparable levels of diversity were found in Massachusetts with 16 to 21 species of ferns and other “fern allies” per hectare reported for four sites (Tryon 1989). Our species list increases to 22 species if we include the 3 fern allies recorded in the hectare (*Equisetum arvense* L., *Equisetum pratense* Ehrhart, *Huperzia lucidula* (Michx.) Rothmaler). One hectare of tropical rain forest in Ecuador contained 50 species of ferns and fern allies, of which 25 were ground-rooted species and 25 were epiphytes (Poulsen and Nielsen 1995). The Mont St. Hilaire plot is therefore comparable to tropical rain forest in the diversity of ground-rooted ferns, perhaps because of the undisturbed nature of the forest, the high level of environmental heterogeneity within the hectare and the fine resolution of our survey. If every hectare of the reserve could be surveyed at the metre scale the observed species richness of some sites would increase, although 19 species is probably near the upper limit.

There are large differences in abundance among fern species in the plot; the number of square metres occupied (R) ranges from 1 to 1231 (of a total of 10 926), while the number of stems (r) is even more variable, ranging from 3 to 13256. Both measures of frequency are highly right-skewed; as in most biological communities the majority of species are relatively rare and a logarithmic transformation of abundance is appropriate (Preston 1948, 1962). As one would expect, there is a strong correlation between R and r ($r^2 = 0.84$) since they express the same quantity at different scales. We have used the average number of stems per m^2 , calculated by r/R , as a measure of growth habit which corresponds to our observations in the field of the tendency of different species to form dense clumps. These values were used to classify each species as either rhizomatous (forming large, dense clumps of stems in which individual plants are difficult to distinguish) or caespitose (branching from a single point to form distinct crowns - which may or may not be truly separate individuals) (Table 1).

Each species was characterized by a distinctive spatial distribution; six examples are presented in Fig. 2. Many species were restricted to specific locations within the hectare, such as *Gymnocarpium dryopteris* along the foot of the slope, *Osmunda cinnamomea* in the low, wet corner and *Dryopteris marginalis* principally in the steeper sites. The degree of aggregation also varied among species as expressed by the coefficient c which ranged from 0.17 for the highly dispersed *Dryopteris intermedia* to 0.007 for the highly clumped *Cystopteris bulbifera* (Table 1, Fig. 2). Highly clumped distributions may result from either a rhizomatous growth habit or a high degree of environmental specificity combined with a patchy distribution of suitable sites.

The aggregated distributions of species within the hectare contribute to the form of the species-area relationship. The curve increases nearly linearly with a slope of 0.40 on logarithmic axes (Fig. 3). Compared to the real curve, the null model of random species distributions produces a more rapid increase in species number with area, although the two lines necessarily converge at the limit. The difference between the curves represents the contribution of spatial structure, or species aggregation, independently of sample size.

Associations among species

The variance of species richness among quadrats is higher than expected from a random distribution at all scales except the 1 m scale (Table 2). These results indicate that some sites are hotspots for species diversity, as opposed to a relatively even distribution of species among sites. At the one-metre scale, the very small size of quadrats is likely to limit the number of individual plants which can exist within a quadrat, such that 94 % of quadrats contain 0 or 1 species and the variance among quadrats is low. The expected variance for a random distribution is actually higher than the observed variance since the occurrence of any species in a square is independent of species already found there (Palmer and van der Maarel 1995). Randomization of the species by sites matrix causes species to occur both randomly and independently whereas the variance test assumes only

Figure 2. The spatial distributions of six species in the hectare. Orientation of the hectare is as in Fig. 1. A. *Dryopteris intermedia* is dispersed throughout the hectare; B. *Cystopteris bulbifera* is restricted to alkaline soils of the moderately sloping corner; C. *Gymnocarpium dryopteris* occurs along the base of the slope, D. *Osmunda cinnamomea* is restricted to the wet area; E. *Dryopteris marginalis* is found on the rocky slope; and F. *Polystichum acrostichoides* occurs along the flat, dry portion of the plot.

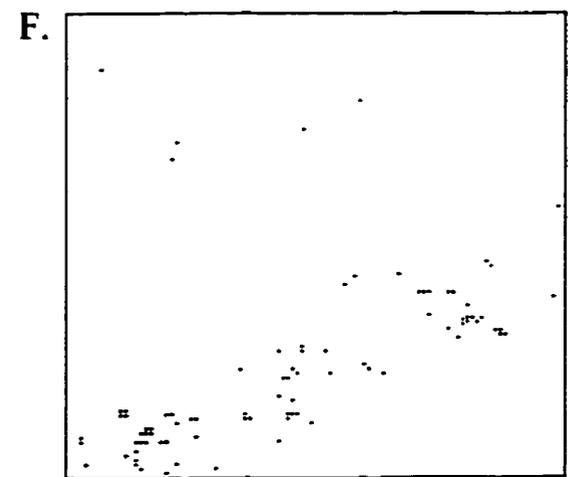
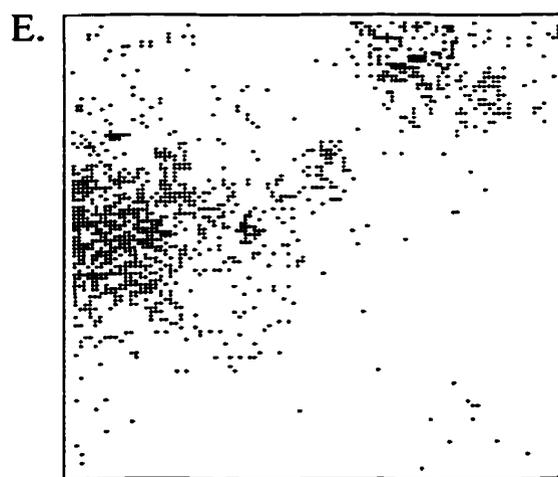
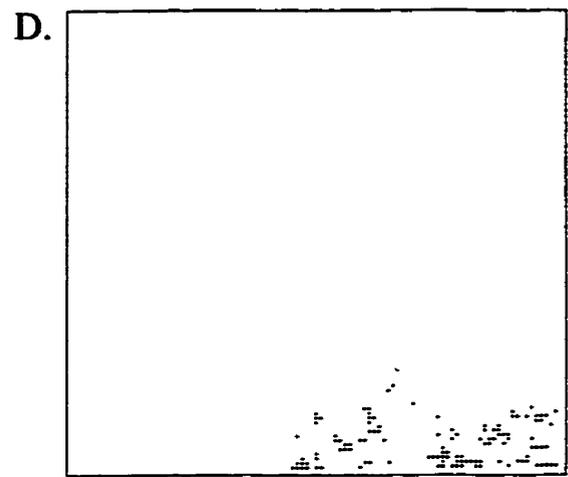
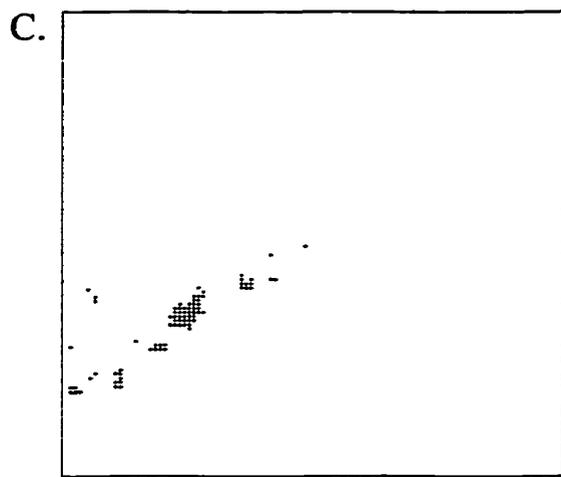
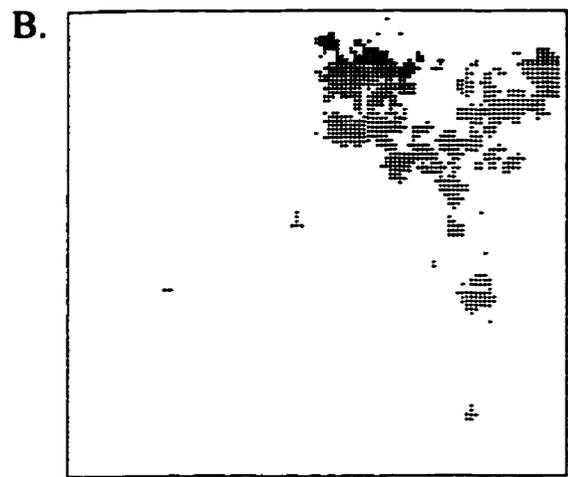
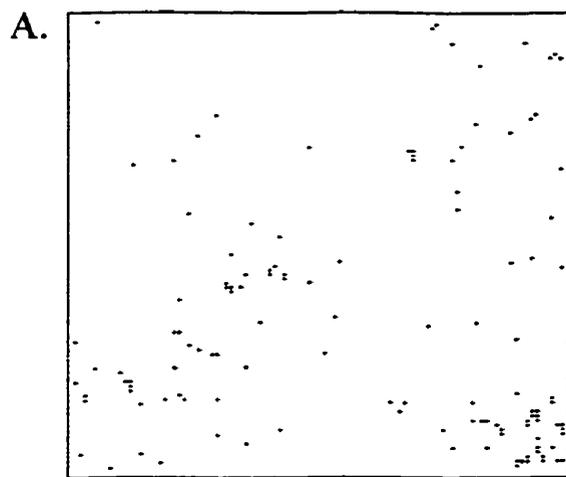


Figure 3. Species-area curves created by aggregating metre quadrats, for real data and for the null model of a random distribution of species among sites.

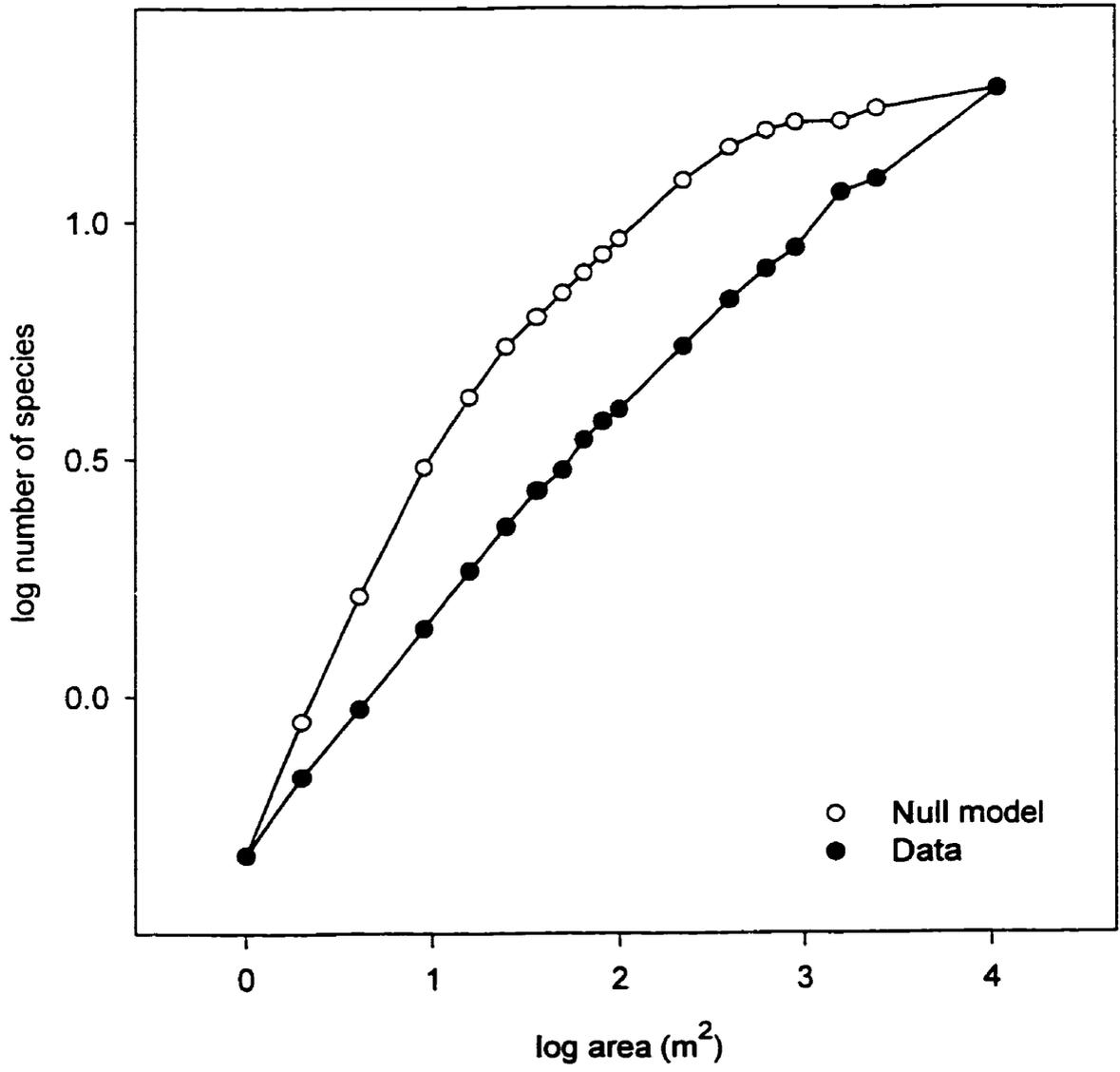


Table 2. Comparison of the variance of species richness among quadrats of different sizes for the data (observed), for the random expectation based on each species' abundance, and for the average of 100 randomisations of species' occurrences (null model). The ratio of observed to expected variance expresses the degree to which the data differ from a random expectation.

	1 m ²	25 m ²	100 m ²	225 m ²	400 m ²	625 m ²
Observed variance	0.40	1.92	3.53	5.57	5.56	5.26
Expected variance	0.42	1.60	2.29	2.62	2.74	2.73
Variance of null model	0.42	1.62	2.29	2.54	2.78	2.93
V_o/V_e	0.95	1.20	1.54	2.13	2.03	1.93

that species occur independently. In this case there appears to be little difference between the two null models (Table 2).

The average specific correlation between pairs of sites as a function of distance expresses the change in species composition through space. The patchy distribution of species produces a decrease in the correlation with distance, as widely separated sites tend to have more different species than neighbouring sites (Fig. 4A). For the null model of random distribution, the correlation-distance relationship is a flat line without any distance decay (Richard et al. *subm.*). Rhizomatous species are more likely to exhibit very aggregated distributions, so we examined the correlation-distance curves for rhizomatous and caespitose species separately. The rhizomatous species have a steeper slope indicating a more coarse-grained distribution with greater similarity of neighboring sites (Fig. 4A). The two curves converge beyond a distance of about 10 m, which presumably represents the maximal extent of clonal spread. Both groups of species had lower correlation values than the curve for all species combined, because of the smaller total number of species involved. Because the specific correlation between quadrats decreases with distance, we observe a corresponding increase in the species richness of two quadrats with distance (Fig. 4B). The curve for rhizomatous species is steeper since the large, dense clumps formed by single species tend to cover several square metres and depress the initial diversity of adjacent sites. The species-distance curve for all species combined has a much higher elevation than either the rhizomatous or caespitose groups because there are more species in total.

The species by species matrix analysis indicated that certain species occurred together much more often than expected by chance while other species had strong negative associations. AFF is positively associated with DCA, OCI and PAC, while DCA also co-occurs with DIN, OCI and GDR (refer to species acronyms listed in Table 1 or Fig. 5). CBU and APE also tend to occur together, whereas DMA occurs much less frequently with APE, PAC and AFF than expected by chance. These relationships can be expressed as a dendrogram in which species were clustered based on the deviation from random expectation of their number of co-occurrences (Fig. 5). This tree diagram was

Figure 4. A. The average correlation between two 1 m quadrats as distance increases, based on species' presence and absence. B. The average number of species in two 1 m quadrats as distance increases. Curves for all species are compared to subgroups consisting of only rhizomatous or caespitose species; slopes of the curves reflect the rate of change of species composition with distance.

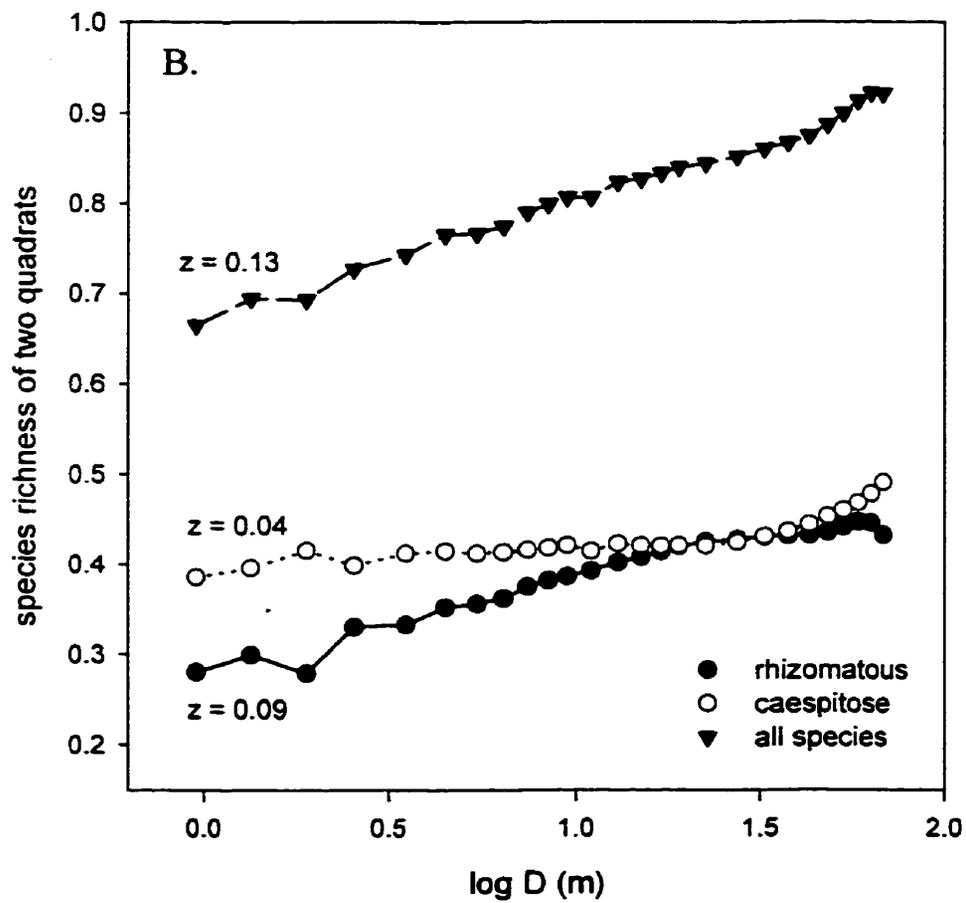
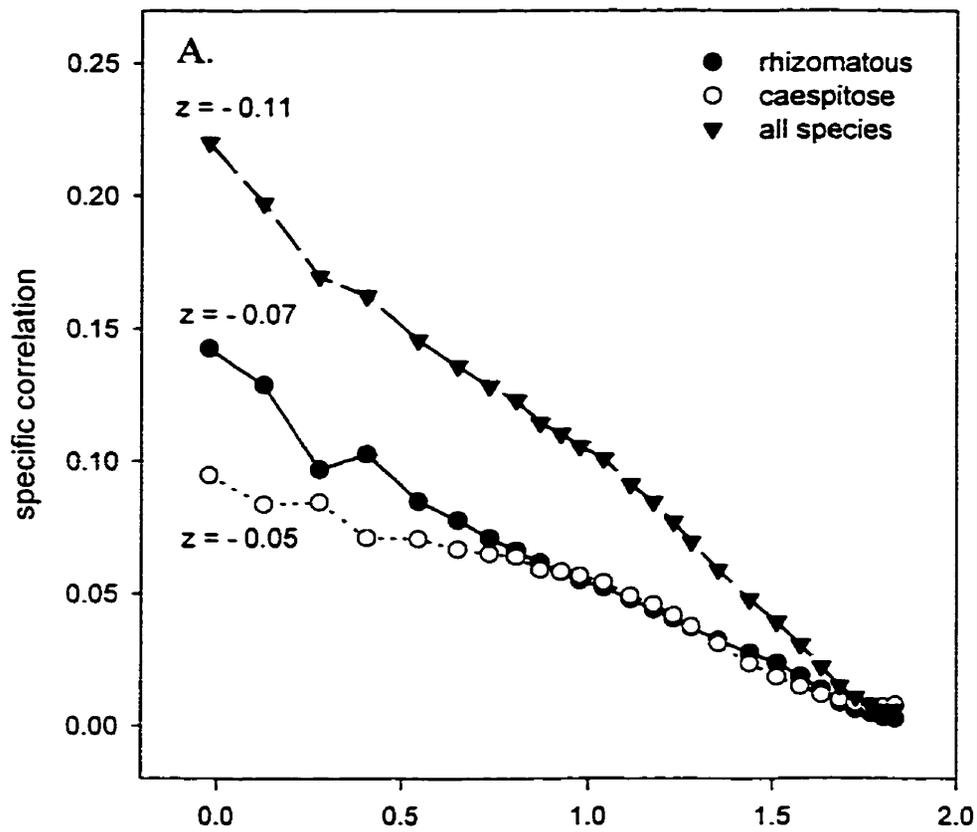
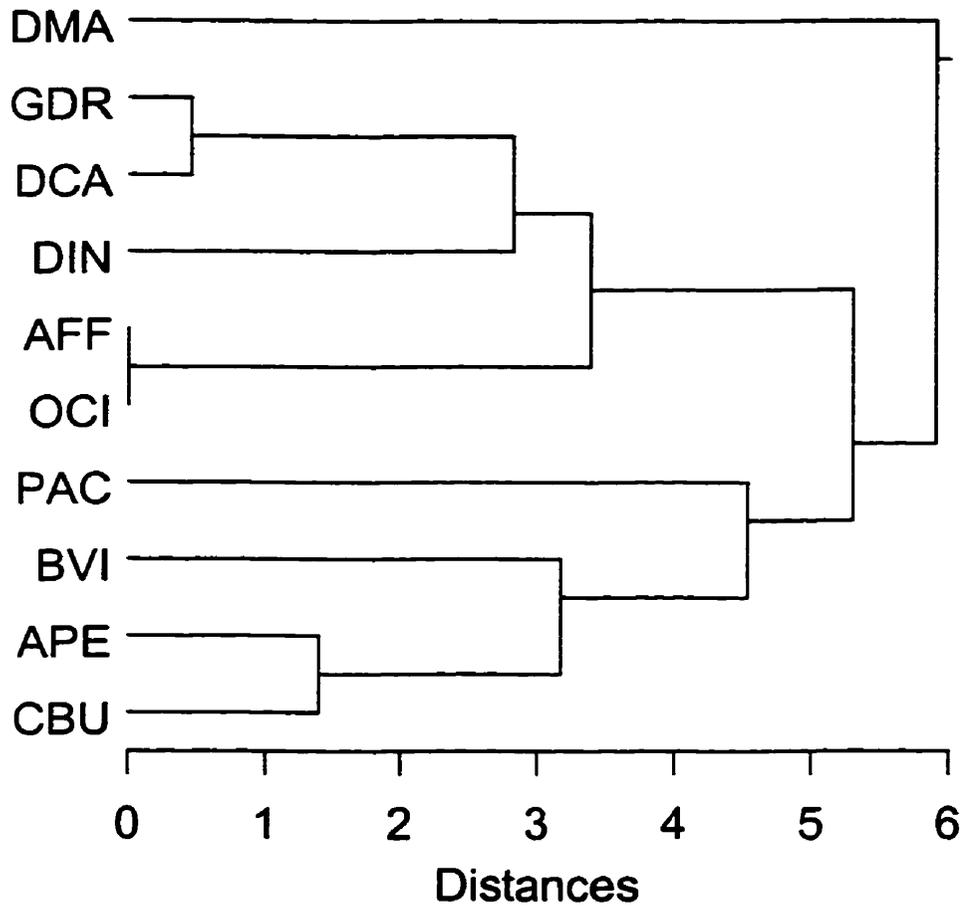


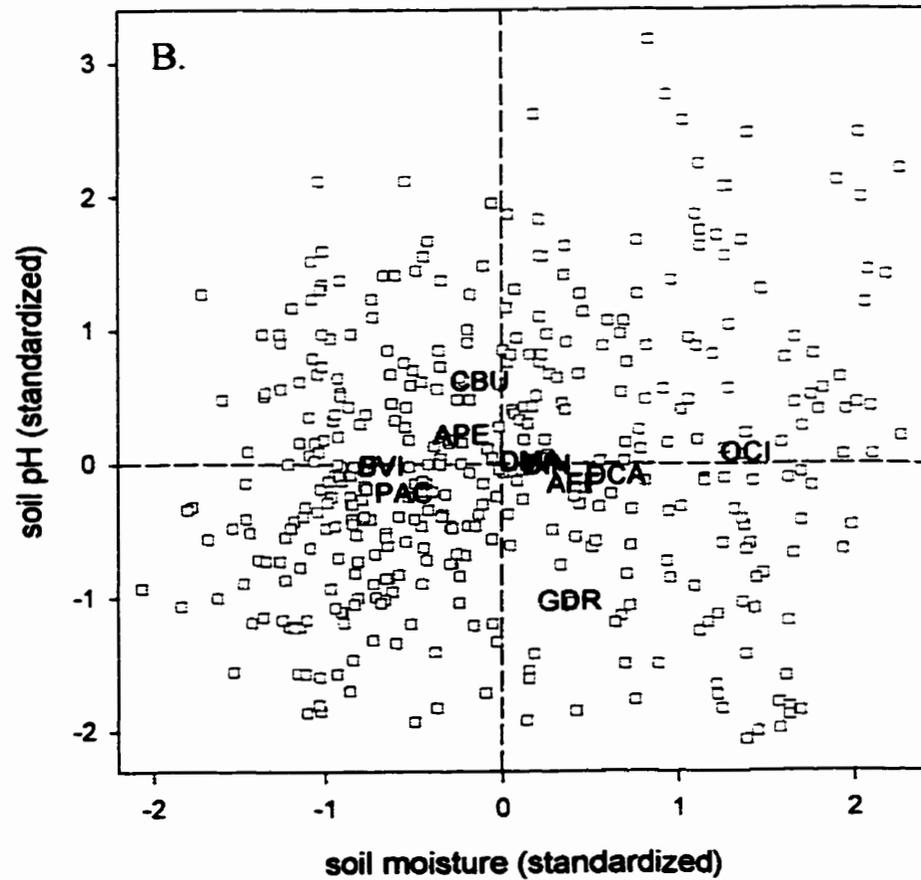
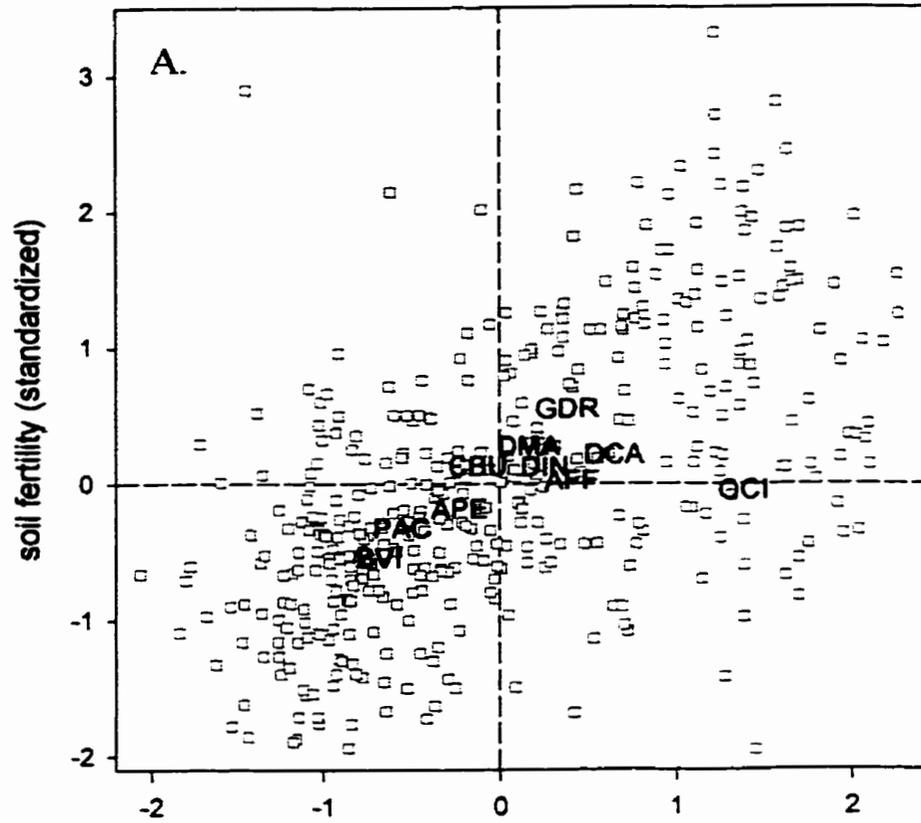
Figure 5. The similarity of species' spatial distributions illustrated as a majority consensus tree. Similarity measures were based on the deviation from random expectation of the number of co-occurrences of each pair of species in 5 m quadrats. DMA = *Dryopteris marginalis*, GDR = *Gymnocarpium dryopteris*, DCA = *Dryopteris carthusiana*, DIN = *Dryopteris intermedia*, AFF = *Athyrium filix-femina*, OCI = *Osmunda cinnamomea*, PAC = *Polystichum acrostichoides*, BVI = *Botrychium virginianum*, APE = *Adiantum pedatum*, CBU = *Cystopteris bulbifera*.



based on a centroid linkage method; it also expresses the consensus of six trees constructed using different clustering methods. APE-CBU-BVI, AFF-OCI and DCA-GDR-DIN formed consistent groupings in all trees, and the latter two groups were joined in 5/6 trees. PAC is joined to the APE-CBU-BVI group in 5/6 trees; in the final case PAC is joined to the larger group of 5 species, probably due to its positive correlation with AFF. The most abundant and most spatially distinct of the 10 species, DMA, branches first and outside of all other groups in 3/6 trees, and is otherwise joined outside or within the group of 5 species due to a higher than expected correspondence with GDR. The species within a group tend to cluster in particular areas within the hectare such that the number of groups at two sites increases with distance, providing a basis for the decrease in the specific correlation with distance (Fig 4A). However, we found that the species richness of two sites also increases with distance within a single group, because each species in a group still has a unique spatial distribution.

The relatively similar spatial distributions of species within the groups identified in Fig. 5 may be due to shared environmental preferences or to some unidentified interaction among species. The environmental preferences of each species, based on the mean soil conditions of all 5 m quadrats where they were found, are shown in Figures 6A and 6B. The association between CBU, BVI, APE and PAC appears to be based on environmental preference, since all four species are found in sites with low soil moisture and relatively low soil fertility. The six other species, while separate from the first four, do not form such a tight group: OCI prefers sites with high soil moisture, whereas GDR prefers sites with high fertility and very low pH. *Dryopteris marginalis* has roughly average preferences for the three soil variables, although its spatial distribution sets it apart from all other species. The nine rarest species were not included in the graph because their environmental scores are based on fewer than 20 samples. However, they tended to fall within the cluster of points formed by the 10 common species, with the exception of *Pteridium aquilinum* which had the lowest moisture and fertility preferences and the second-lowest (after GDR) pH preference of any species. Spatially, *P. aquilinum* is restricted to the north-east corner of the hectare, suggesting a high positive association with DMA. *Cystopteris fragilis* seems to belong with the APE-CBU-BVI-PAC group,

Figure 6. Soil preferences of each species based on the mean soil conditions of all the sites occupied by that species, expressed in units of standard deviation from the mean. Species acronyms are the same as in Fig. 5. These average preferences are compared to the range of conditions found in all 5 m quadrats (open squares). A. fertility vs. moisture. B. pH vs. moisture.



while the remaining species are found with the group occupying the wetter, south-west portion of the site. Figure 6 also shows that ferns as a whole occupy sites with generally average soil conditions for this particular hectare, although there is more variation among species for soil moisture preference for than for pH or soil fertility. At the 1 ha scale, Bell and Bernhardt (in prep.) found that fern species occupied quadrats with higher water accumulation and lower solar radiation values compared to the average for all sites.

We may expect species with a narrow tolerance for environmental conditions to be restricted to certain sites and thus more patchily distributed. If so, there should be a positive relationship between the dispersion of a species as measured by the coefficient c , and its environmental tolerance as measured by the variance of soil conditions in all sites where a species occurs (σ^2_E). There was no relationship between these two characteristics (Fig. 7), however, the arrangement of species suggests several groups of distribution types. The most highly dispersed species are all caespitose and have a wide range of environmental tolerances. The 5 most common rhizomatous species exhibit clumped distributions, as well as relatively low environmental variance. Finally, three caespitose species (OCI, AFF, DMA) have low dispersion values suggesting an apparent spatial limitation, without particularly low environmental variance levels.

Environmental structure

Soil conditions varied widely within the hectare: soil moisture ranged from 13.4 to 86.8 % among the 400 samples (mean 48.4 %); soil fertility by bioassay with *Chlamydomonas* varied from 0 to 659 (mean 245); soil pH varied from 4.3 to 8.2 (mean 7.2). In the absence of replicate samples we cannot straightforwardly calculate environmental variance, but all three variables show evidence of spatial autocorrelation, as log variance increases with log distance (Fig. 8). The slope for soil moisture (0.31) is higher than for pH (0.20) and soil fertility (0.14), indicating that soil moisture has the most coarse-grained distribution (the largest patch size) of the three variables.

Figure 7. The relationship between the spatial dispersion of a species, c , and the variance of environmental conditions of the sites where it occurred (variance is a composite value based on the variance of soil moisture, fertility and pH). Species acronyms are the same as in Fig. 5.

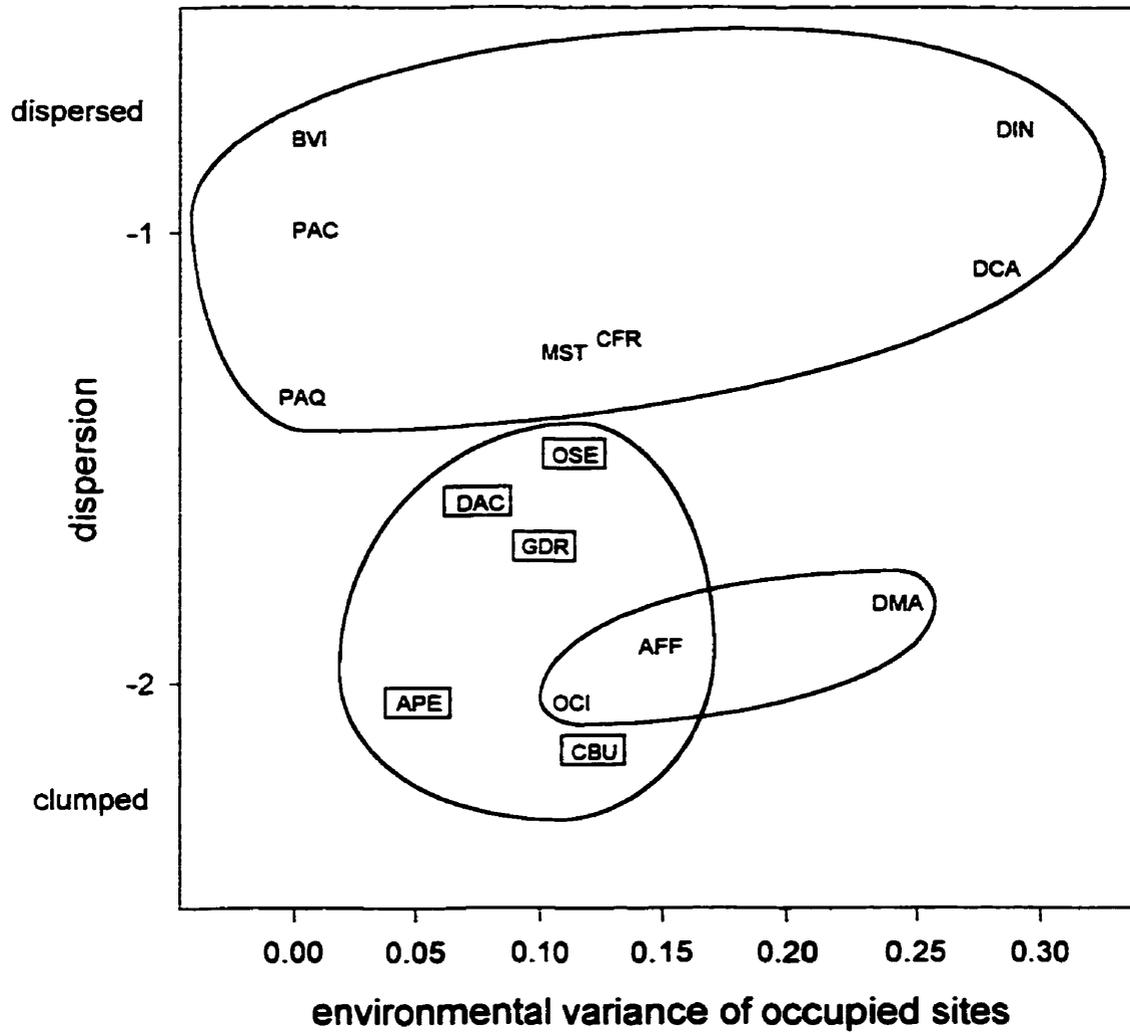
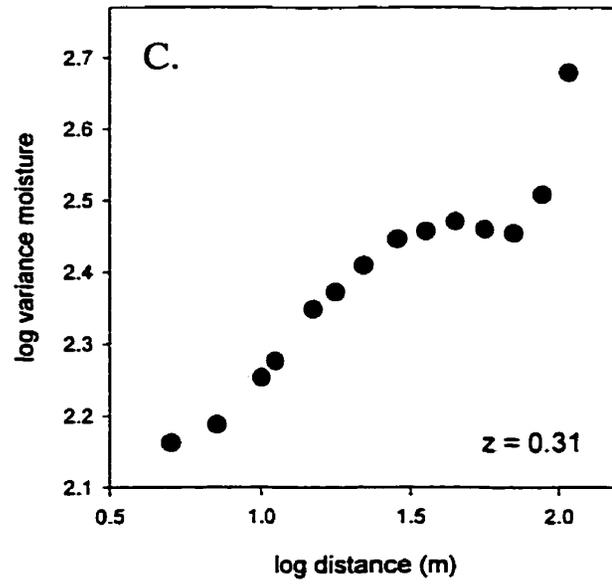
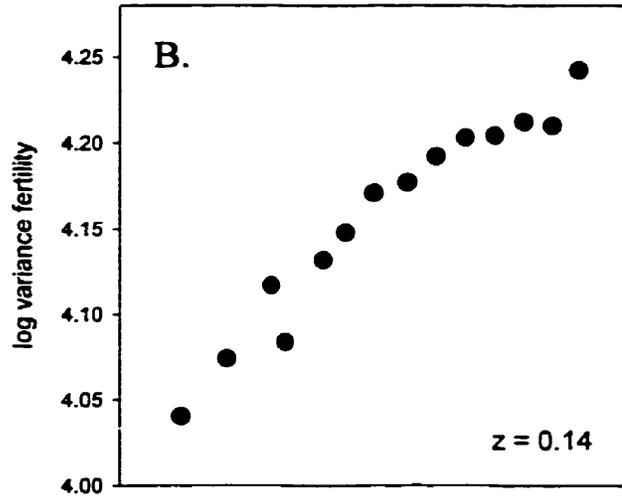
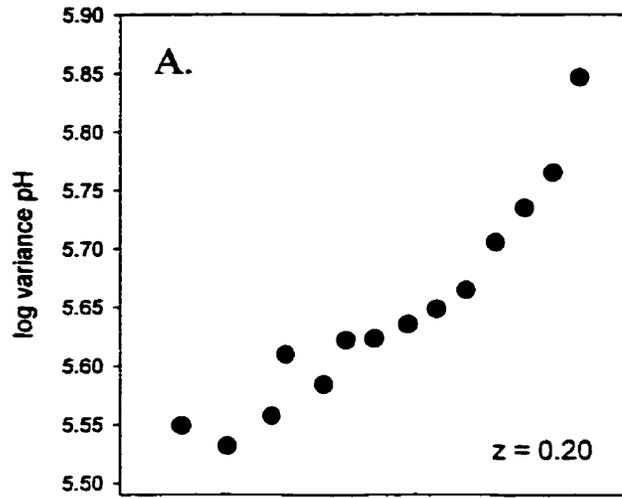


Figure 8. Average variance of environmental conditions among quadrats as distance increases. A. soil pH, B. soil fertility, C. soil moisture.



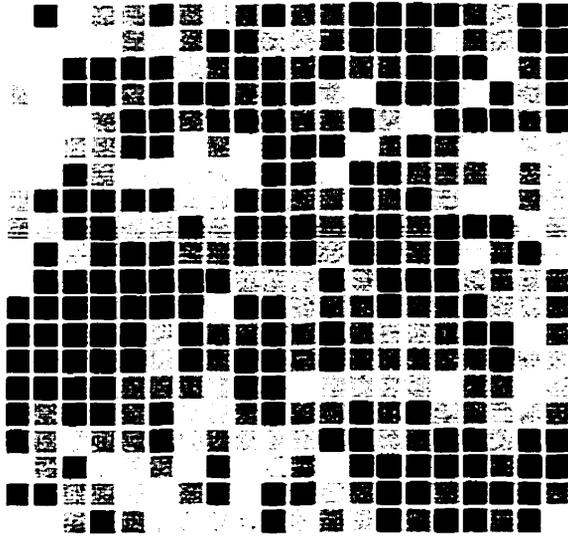
The patchy distribution of environmental conditions and of diversity is best appreciated from maps (Fig. 9). The strong topographic gradient which characterizes the hectare appears to influence the other physical and soil characteristics. Moisture levels are highest in the low, south-west corner and in a band following the foot of the slope. Soil fertility appears positively related to soil moisture in the sloping half of the hectare, but is not particularly high in the wet corner. The distribution of pH is distinct from the other two variables: the south-east quarter of the hectare contains a large area of very alkaline soil corresponding to a shallow valley which appears to be a temporary stream bed. Acidic soil occurs along the northern portion of the site, on the steepest part of the slope and along its base. Relationships among soil variables are weak overall, although soil moisture and soil fertility are positively correlated ($r^2 = 0.32$). At the 5 m scale, species richness ranges from 0-6 species, and is especially low in the steepest corner of the plot. Diversity hotspots appear to be the wet, south-west corner and the relatively dry south-east corner characterized by a gentle slope and a dry stream bed.

Environmental variation and diversity

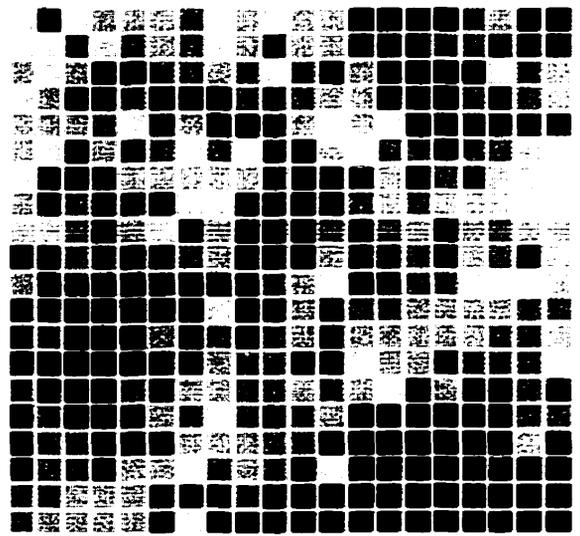
Fern diversity was strongly related to mean soil conditions in the multiple regressions (Table 3). Diversity was greater at sites with high moisture and low fertility, although these two variables were positively correlated with each other. Soil moisture and fertility were significant at all scales and for all replicate versions of the grid. The amount of variation explained increased with scale, from an average r^2 of 0.09 for the three 5 m grids to an average r^2 of 0.52 at the 25 m scale. At smaller scales, diversity was also negatively related to the mean abundance of rock and wood, probably due to a lack of space or soil for plant growth in areas with a high proportion of rock or wood. The amount of mud was positively related to diversity because many species occur mainly in the wet south-west corner of the hectare where the mud and water are located. The effect of physical variables on species richness disappears at scales larger than about 15 m. Contrary to expectation, the variance of physical and soil characteristics do not explain variation in diversity. Although in a few cases environmental variance appears significant, the patterns are inconsistent and not robust to shifting of the grid. Thus, even

Figure 9. The spatial structure of soil conditions and diversity among 5 m quadrats of the hectare. Shades of grey indicate environmental measures from low to high values. A. Soil fertility varies from 0 to 659; B. soil moisture varies from 13 to 87 %; C. pH varies from 4.3 (dark) to 8.2 (light); D. the number of species varies from 0 to 6. Orientation of the hectare is as in Fig. 1.

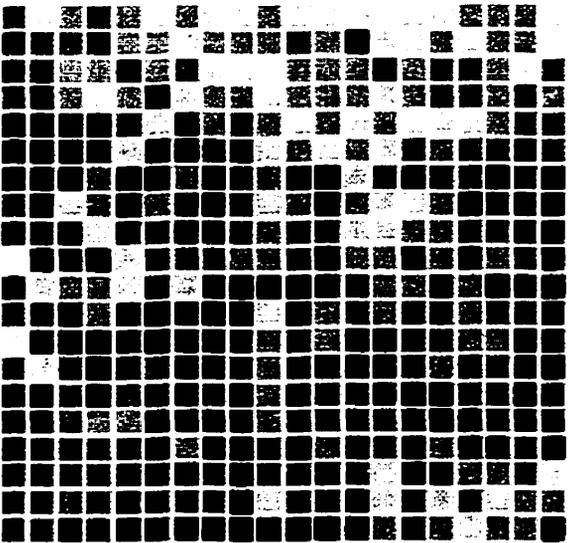
A. Fertility



B. Moisture



C. pH



D. Diversity

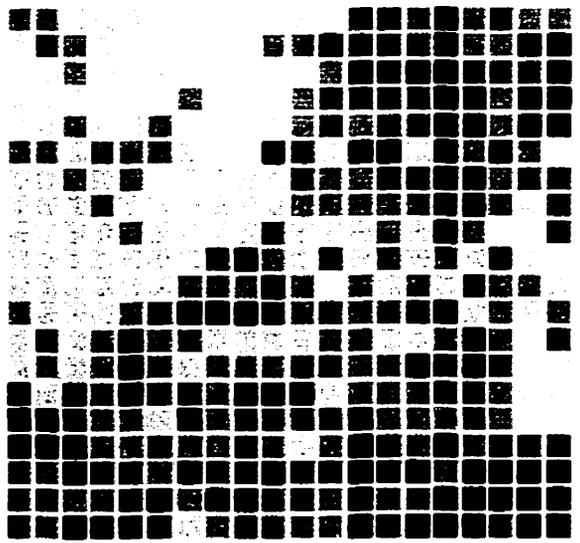


Table 3. Environmental factors which were significantly related to species diversity in multiple regressions (significance level ≤ 0.05). The number of stars indicates the number of replicates in which the variable was significant; the (+) or (-) symbol denotes positive or negative relationships between the variable and diversity.

Scale (m)	Physical means		Physical variance		Soil means		Soil variance	
5 x 5	***	rock (-)	*	wood (+)	***	moisture (+)	N.A.	
	***	wood (-)	*	mud (+)	***	fertility (-)		
	***	mud (+)						
10 x 10	***	rock (-)	*	wood (+)	***	moisture (+)	*	moisture (-)
	***	wood (-)			***	fertility (-)	*	fertility (+)
	***	mud (+)						
15 x 15	*	rock (-)	*	water (+)	***	moisture (+)	*	pH (-)
					***	fertility (-)	*	moisture (-)
							*	fertility (+)
20 x 20	-		-		***	moisture (+)	-	
					***	fertility (-)		
25 x 25	-		-		***	moisture (+)	-	
					***	fertility (-)		

though substantial heterogeneity exists within the hectare and species appear to distribute themselves according to soil preferences, we did not observe an effect of environmental variance at scales less than one hectare.

We repeated the regressions for the 7 rhizomatous and 11 caespitose species separately with no great change in the resulting patterns. Mean soil fertility and soil moisture remain the strongest predictors of diversity, although moisture is a weaker predictor of caespitose species while fertility is only weakly related to rhizomatous species, with no effect at scales of 20 or 25 m. Mean soil pH has a negative influence on caespitose species and a positive influence on rhizomatous species at small scales. The amount of rock and wood is once again negatively related to diversity of both groups at the 5m scale, but the effect of mean physical conditions remains important at larger scales for the rhizomatous species. A positive relationship between diversity and variance of rock was observed for the rhizomatous species, only at the 5 m scale. Unfortunately, the range of species richness is very low within each subgroup, especially the 7 rhizomatous species, thus decreasing our ability to detect patterns.

Discussion

The existence of a positive relationship between environmental heterogeneity and species diversity depends upon at least two conditions: there must be sufficient environmental variation among sites, and each species must occur in the sites to which it is best adapted and in which it can achieve higher fitness than other species (Bell and Lechowicz 1991). The first condition appears to be fulfilled in our study hectare since physical and soil conditions were both very heterogeneous and spatially structured (Fig. 1, 8, 9). Over time, selection should act to sort each species into sites with the appropriate environmental conditions, through the processes of competition and adaptation. The very distinctive spatial distributions of some species provide indirect evidence for the importance of selection, for instance, species which occur only in the wet corner or only on the slope (Fig. 2). The decrease of the specific correlation between sites with distance

(Fig. 4) reflects this patchiness of species distributions. Moreover, fern species displayed different preferences for soil conditions at the sites that they occupied (Fig. 6).

Dispersal of spores, seeds or juvenile organisms will tend to counteract the influence of selection and disrupt the relationship between diversity and environmental heterogeneity. As propagules disperse from a parent plant or immigrate from outside areas, they tend to be scattered into sites without regard for environmental conditions. This influx of species into sites to which they are not well-adapted has been termed the mass effect (Shmida and Wilson 1985); it tends to inflate the diversity of sites and reduce predictability between species distributions and the environment. The relative importance of either selection or dispersal on the composition of sites should be dependent on scale. Effects of dispersal and immigration may be more likely to predominate at small scales, as the majority of individuals probably disperse over relatively short distances (Auerbach and Shmida 1987). Thus, there should be a certain scale above which the effects of selection begin to dominate and the positive relationship between environmental heterogeneity and diversity emerges; this scale will depend on the life-history of the group under study. The spatial scale at which selection becomes predominant should be larger for organisms with high dispersal abilities than for more sedentary species. At the limit, however, the processes of selection and assortment among suitable sites will be very slow for extremely poor dispersers.

For ferns, the scale at which effects of environmental heterogeneity begin to emerge appears to be slightly larger than 1 hectare. Bell and Bernhardt (in prep.) observed a relationship between species diversity and the variance of solar radiation and topography which became stronger as scale increased above 1 ha. Environmental heterogeneity was not related to diversity in the present study, even though soil properties varied on scales which are relevant to plant growth and dispersal. Ferns are reputed to have virtually unlimited dispersal abilities, especially in comparison with seed plants; their distribution on oceanic islands attests to their spores' capacity for long-distance dispersal and self-fertilization (Tryon 1970). In reality, the vast majority of spores fall near the parent plant, following a leptokurtic distribution (Peck et al. 1990). Moreover,

the sporophytes of many fern species are strong perennials and spread by vegetative growth. The “individual” plants are connected by spreading underground rhizomes, producing either a pattern of separate crowns (ex. *Osmunda*, *Matteucia*) or spreading outward in very dense clumps made up of many stems, in which individual plants can scarcely be distinguished (ex. *Adiantum*, *Gymnocarpium*). Finally, *Cystopteris bulbifera* spreads vegetatively through tiny bulblets on the undersides of its fronds, which fall off and produce new plants. It would be interesting to compare the diversity-environment relationships described here for ferns to a group of organisms with different dispersal strategies.

Despite a tendency for most spores to fall near the parent plant, the sheer volume of spores released by adult sporophytes may still ensure that no sites are lacking ferns for want of spore arrival; rather, there may be limitations at later stages of development. As in most studies, our observations are restricted to the distribution and environmental preferences of sporophytes, but these are dependent on the germination, establishment and survival of gametophytes. Many gametophytes require disturbed soil, followed by prolonged sheltered, damp conditions, such as may occur after a severe rain storm in mid to late summer (Peck et al. 1990). Others such as *Botrychium virginianum* have non-photosynthetic gametophytes and form an association with a fungal symbiont (Soltis and Soltis 1986). The adult fern must grow and survive at the germination site, and may experience different selective pressures than the gametophytic generation. Thus, the distribution of sporophytes may partially reflect the environmental requirements and restrictions of gametophytes.

The dichotomy between sporophytic and gametophytic generations, as well as the opposing forces of selection and dispersal, emphasize the importance of scale in the study of ecological relationships. A closely related issue is the distinction between measured heterogeneity, imposed by our study design, and functional heterogeneity, or the heterogeneity that organisms perceive and respond to (Kolasa and Rollo 1991). We did not observe a relationship between environmental heterogeneity and species diversity in this study, perhaps because the influence of dispersal processes predominates over

selection at this scale. In addition, our scale of measured heterogeneity, chosen because it seemed appropriate for the size of the adult study organisms, may in fact be incongruent with the functional response of a different life-history stage, the gametophyte. The measured heterogeneity, estimated by soil samples collected every 5 m, may not even reflect the functional heterogeneity perceived by adult ferns since it has been shown that soil conditions vary on much finer scales than 5 m squares (Robertson 1988, Palmer 1990, Lechowicz and Bell 1991). If species are restricted to very specific soil types but high soil heterogeneity occurs within quadrats, then the environmental tolerance of each species will be overestimated using mean soil conditions (Palmer and Dixon 1990). The boundaries of "habitats" (patches of particular conditions) or of "communities" (groups of associated species) will continually change as a function of the scale of observation. It is important to operationally define the system under study to foster more effective comparisons among studies and greater progress in developing and testing hypotheses (Palmer and White 1994a).

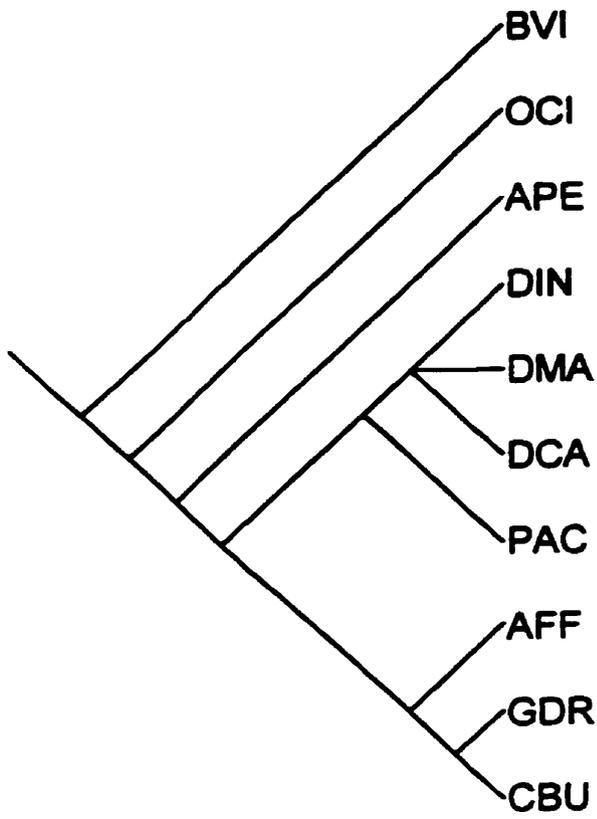
Although there was no relationship between diversity and variance of the environment, diversity was influenced by mean conditions of soil moisture and soil fertility. The positive relationship with moisture probably occurs because more individuals and species prefer to grow in wet sites; it is generally recognized that most ferns enjoy damp, shady places. Bell and Bernhardt (in prep.) also found that the diversity of 1 ha quadrats was highest for sites with low solar radiation and high flow accumulation, and those which contained ponds, streams or seeps. The negative relationship between diversity and soil fertility is more puzzling. Diversity is often observed to be a unimodal function of productivity; this humped relationship thus reconciles studies which have observed either positive or negative relationships between diversity and productivity (Rosenzweig 1995). However, a decline in diversity is typically observed for extremely nutrient-rich systems such as fertilized fields (e.g. Tilman 1987). It is possible that fern species are being excluded from rich sites by competition with other plants. Interspecific competition is of primary importance in the organization of plant communities, at least at local scales (Tilman 1982, Keddy 1989). Unfortunately, little is known about competition among ferns or between ferns and other

plants, and this idea cannot be tested without information on the distribution of other understory species.

One other factor which can be related to species distribution patterns are the phylogenetic relationships among organisms (Gaston et al. 1997). With information on species and sites from a biological survey, we can consider a non-spatial analogue to the species-area curve: the relationship between phylogeny and range size. In the former, as sites are added we observe an increase in total species richness, while in the latter, species are added sequentially to produce an increase in the total number of occupied sites. At certain scales or taxonomic levels, more closely related taxa may be observed to have more similar spatial distributions than distantly related taxa - a sort of genetic distance decay. Figure 10 depicts the phylogenetic relationships among the 10 common species of the hectare (based on analyses by Wolf et al. 1994, Hasebe et al. 1995, Pryer et al. 1995). The main clades are the group formed by AFF-GDR-CBU and that consisting of the *Dryopteris* species plus *Polystichum*, while BVI, OCI and APE branch off earlier. At this scale, these phylogenetic groups do not appear to correspond with the groupings identified by similarity of spatial distribution.

In summary, we have shown that environmental conditions and species diversity are both spatially structured and that significant positive and negative spatial associations exist among species. Species diversity was higher at sites with high soil moisture and low soil fertility. Diversity was not related to environmental variance, probably because at this small scale the opposing force of dispersal processes, and possibly biotic interactions, exerted a stronger influence on distribution patterns. Continued comparative surveys should evaluate the relative importance of different processes affecting diversity as scale changes and examine how the dispersal ability of organisms affects their response to environmental heterogeneity.

Figure 10. Phylogenetic relationships among the 10 most common species based on analyses by Wolf et al. 1994, Hasebe et al. 1995, Pryer et al. 1995.



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Chapter 2

The contribution of scale and structure to spatial patterns of fern diversity

Abstract

Species diversity patterns such as the species-area curve and species turnover from place to place are determined by the complex arrangement of species among sites. In this study, we isolate effects of spatial scale and spatial structure on diversity patterns by comparing nine biological surveys of fern distributions to null models in which species are distributed randomly in space. Nearby sites are more similar to each other than distant sites, such that the correlation in species composition between two sites declines with distance. Consequently, the combined species richness of two sites initially increases with distance, although a decline often occurs beyond a certain point. Species-area curves increase more slowly for real data than random data due to the effects of spatial structure. Diversity patterns are affected by different components of spatial variation, including the aggregation of species, the spatial structure of diversity hotspots and the associations among species, as well as by the number of quadrats in the survey. The slopes of species-area curves and correlation-distance curves were generally similar across surveys ranging in scale from 1 x 1 m quadrats covering one hectare to 50 x 50 km grid squares covering Western Europe. Regularities in diversity patterns may be related to the approximately constant distribution of abundance (range size) at all scales; in contrast, there were marked differences between surveys in the frequency distribution of species richness. Comparative studies of a variety of taxonomic groups and geographical areas will provide useful estimates of spatial variation and species turnover, allowing the improvement of theoretical models and the prediction of diversity in poorly-known areas.

Introduction

The relationship between species richness and area is the oldest and best-known diversity pattern (Rosenzweig 1995). From a theoretical viewpoint, a solid understanding of how and why the number of species in a survey increases with area provides insight into the evolutionary and ecological processes which structure communities (Connor and McCoy 1979, Condit et al. 1996). On a practical level, species-area curves have been used in conservation biology to predict the loss of species expected from a given decrease in habitat area (Diamond 1975, Pimm et al. 1995). Consequently, the explanation and prediction of species-area curves are central issues in ecology and have fueled a vast number of experiments, empirical studies and theoretical models (reviews in Connor and McCoy 1979, Williamson 1988, Rosenzweig 1995).

Two main types of explanations have been proposed to explain the positive species-area curves observed in nature. Higher species diversity levels in larger areas are thought to be caused by either a greater number of individuals or a greater variety of habitats. These contrasting hypotheses represent effects of spatial scale and spatial structure, respectively. The individual-based explanation, also referred to as the *area per se* hypothesis (Connor and McCoy 1979, Nilsson et al. 1988), assumes that larger areas will support more individuals and therefore more species. Those species will have larger population sizes and a corresponding decreased risk of extinction. This hypothesis has been formally developed as the theory of island biogeography (MacArthur and Wilson 1967), and can be considered a neutral model of community organization since it is based on colonization-extinction dynamics and does not assume that species differ in competitive ability, growth rates or other characteristics (see also Hubbell and Foster 1986, Hanski and Gyllenberg 1997). In contrast, the habitat hypothesis assumes that larger areas contain a greater number of distinct environmental conditions than small areas, permitting the coexistence of more specialist species (Williams 1964, Shmida and Wilson 1985). This functional hypothesis relies on the existence of environmental heterogeneity as well as on the adaptation of species to their local milieu where they are able to attain higher fitness than their competitors. The dichotomy between the neutral and functional theories of species-area relationships is analogous to the debate between

neutral and selection-based models in the genetic literature (Lewontin 1974). Hypotheses based on scale and structure are not mutually exclusive: both processes are likely to influence species diversity in a given area and their relative importance may vary depending on the overall spatial scale examined (Auerbach and Shmida 1987). The general objective of this study is to separate the effects of scale and structure on diversity patterns within contiguous regions in an attempt to quantify the importance of spatial structure as evidence for the functional hypothesis of species diversity.

Pure scale effects are sufficient to produce a positive species-area relationship. Consider a hypothetical region in which all species occur randomly, without any correlation between their distributions. This pattern of species occurrences can be considered homogeneous at a regional scale since there is no difference on average between sites which are close together and those which are far apart. The probability of encountering a given species is equal at every site in the region and is simply a function of that species' abundance. If small quadrats close to the size of individual organisms are surveyed, then the first individual collected will increase the number of species from zero to one, producing an initial increase in the species-area curve with a slope of one. As more quadrats are added, the number of individuals and species will accumulate, and the species-area curve will continue to increase but with a progressively decreasing slope determined by relative species abundance levels (Coleman 1981, Coleman et al. 1982). Therefore, sampling in a homogeneous landscape will produce a positive species-area curve based on scale alone.

In reality, species do not occur randomly but are spatially aggregated at every scale (Taylor et al. 1978). Patchy species distributions occur for a variety of reasons, including spatial and temporal heterogeneity of environmental conditions and biotic factors such as dispersal and competition (Auerbach and Shmida 1987). The spatial structure of species distributions in the study region will have important consequences for diversity patterns. Environmental variables are known to exhibit spatial autocorrelation, so that nearby sites are more similar to each other than distant sites (Bell et al. 1993). If species distributions reflect preferences for particular environmental conditions or

habitats, then species composition should also become more different among sites as distance increases. The similarity of species composition for a pair of sites can be calculated as a binary correlation between species' presences and absences; this specific correlation should decline with distance, becoming negative once the species found at one site tend to be absent at the other site. If the correlation between sites declines with distance, we expect a corresponding increase in the combined number of species found at any two sites as distance increases. The rate of decrease in specific correlation with distance and the rate of increase in species richness with distance reflect the level of spatial heterogeneity or structure in species distributions. Both these structure functions would be flat if species occurred randomly throughout the study region.

The aggregation of species in a region will affect the form of the species-area relationship. Spatial structure decreases the slope of the species-area curve initially, since fewer species are encountered for every given increase in area, compared to a random distribution. Empirical results indicate that species-area curves often rise linearly according to a power law relationship of the form: $S = cA^z$, which can also be expressed as $\log S = \log c + z(\log A)$ (Connor and McCoy 1979, Rosenzweig 1995). The slope of this relationship (z) is a function of the degree of species aggregation (Caswell and Cohen 1993). In comparison, a species-area curve based on a random arrangement of species will increase more steeply initially, but will progressively curve downwards and converge with the aggregated data at the extreme right end of the line, which includes all species in the region. This pattern has been known at least since Gleason (1922) showed that disaggregated quadrats accumulate species more rapidly than nested ones. However, there appear to have been few attempts to explicitly isolate the effects of structure and scale on species-area curves by comparing real data to null models of random distribution.

The first objective of this study is to examine the relative contribution of scale and structure in producing empirical diversity patterns. For a series of biological surveys of fern species, we examine species-area curves, correlation-distance curves, species-distance curves, the distribution of species richness among sites and the distribution of

range size among species. These patterns are compared to null models in which the species occurrences have been converted to various types of random distributions, allowing us to isolate the contribution of spatial structure from pure scale effects. Ferns are an appropriate taxonomic group since their mobility should be less limited by dispersal than many plant groups. The spores of ferns are abundant, light and easily dispersed over large distances; moreover, ferns are independent of pollinators and seed vectors (Tryon 1970, Barrington 1993). Therefore, the spatial arrangement of fern species should be predominantly determined by habitat heterogeneity, or the environmental conditions the spores encounter where they land (Tuomisto and Poulsen 1996).

Our second objective is to examine how diversity patterns are affected by the spatial scale of a survey. In this sense, *scale* refers to the sampling resolution and total extent of the survey rather than a larger sample size. The scale-dependence of ecological patterns has important implications for our understanding of community dynamics (Ricklefs 1987, Levin 1992). The data sets of fern distributions examined in this study encompass a very broad range of spatial scales, from local forest communities to the whole of Western Europe. The surveys differ in both total extent or maximal distance covered, and grain or quadrat size which varies over nine orders of magnitude. Palmer and White (1994) have attempted to clarify the functional form of the species-area relationship by separating the effect of area into the components of grain and extent. They conclude that both grain and extent, as well as their interaction, influence the form of the species-area curve and that the slope is highly dependent on scale. A more complete characterization of the behavior of species-area curves over a broad range of scales would be useful in identifying the relative importance of spatial structure and area *per se* in determining the curve's form. We investigate how diversity patterns behave at different scales by addressing the following questions: How does the distribution of species richness and the distribution of range size vary among surveys conducted at different scales? How does the level of spatial heterogeneity of species distributions change? How are the slope and elevation of the species-area, correlation-distance and species-distance curves affected? Are patterns similar across a wide range of scales, or do we observe consistent changes as scale increases?

Methods

The surveys

We compared the spatial diversity patterns of fern species from nine systematic grid surveys (Table 1). The grid system has become widely used as a means of representing species ranges and as a convenient framework for organizing biological surveys and atlases (Gaston 1994a). The principal objective of this sampling design is to survey every grid square consistently, irrespective of its accessibility or botanical interest, thus reducing the incidence of false negatives inherent in traditional dot maps based on sporadically acquired museum or herbarium specimens. Two of the data sets were field censuses of fern distributions conducted at Mont St. Hilaire, a relatively undisturbed old-growth forest reserve in southern Quebec. The first survey (hereafter referred to as MSH 1) was conducted in 1996 and recorded the number of fern species in each hectare of the forest (Bell and Bernhardt in prep.). Using a detailed topographical map overlaid by a grid, field researchers oriented themselves to the center of each hectare and then walked four loops through the hectare, one in each quadrant, recording all species of ferns. The second survey (MSH 2) was conducted in 1997 and consisted of a metre-level census of a single hectare; the study plot encompassed a wide variety of environmental conditions from a low, wet area to a dry, rocky slope (Richard et al. in prep). Within the hectare, surveying equipment was used to install a regular grid of permanent pins every 10 metres. We then set up ropes around and across the centre of each 10 x 10 m section, delimited individual square metres using marks on the ropes and meter sticks, and counted the number of individuals of each fern species per square metre. The permanent markers were installed 10 metres apart according to an aerial view of the hectare, but since a portion of the plot consists of steeply sloping terrain, some 10 m squares are actually slightly larger on the ground which explains why we obtained 10926 one-metre quadrats in the hectare.

Table 1. Spatial scale and total species richness of the nine biological surveys used in analyses.

Data set	Quadrat size	Quadrat area (km ²)	Number of quadrats	Number of species	Source
Mont St. Hilaire, Quebec (MSH 2)	1 x 1 m	0.000001	10926	19	field survey
Duke Forest, North Carolina	16 x 16 m	0.000256	100	5	Palmer and White 1994
Mont St. Hilaire, Quebec (MSH 1)	100 x 100 m	0.01	1016	38	field survey
Hämeenlinna, Finland	1 x 1 km	1	171	15	Raino Lampinen, unpubl.
Warwickshire, Great Britain	2 x 2 km	4	635	26	Cadbury et al. 1971
Leicestershire, Great Britain	2 x 2 km	4	477	20	Primavesi and Evans 1988
Germany	10 x 10 km	100	2095	56	Haeupler and Schönfelder 1989
Finland	10 x 10 km	100	3090	37	Lahti et al. 1997
Western Europe	50 x 50 km	2500	1522	98	Jalas and Suominen 1972

Besides the two field surveys conducted at Mont St. Hilaire, seven other data sets were assembled for comparison of diversity patterns across a wide range of spatial scale. The Duke Forest survey is most similar in design to our own data, consisting of a detailed census of one hundred 16 x 16 m quadrats in North Carolina (Palmer and White 1994). The survey of the town of Hämeenlinna, inland Southern Finland, was conducted by Raino Lampinen over a period of several years using a grid of 1 x 1 km cells (Flora of the town of Hämeenlinna, unpubl. data provided by Raino Lampinen; draft maps available at www.helsinki.fi/kmus/hml/). The remaining five data bases are surveys of Leicestershire, Warwickshire, Germany, Finland and Western Europe which have relied on the work of a very large number of botanists and naturalists over many years (Cadbury et al. 1971, Jalas and Suominen 1972, Primavesi and Evans 1988, Haeupler and Schönfelder 1989, Lahti et al. 1997). In this type of survey, the geographical occurrences are generally based on available historical records for a species, complemented by more recent censuses which attempt to improve consistency of sampling effort among all quadrats. Some difficulties with this data include incomplete coverage of large squares and overrepresentation of species considered "interesting" by virtue of their rarity or other characteristics (Gaston 1994b). Incomplete species lists and uneven sampling intensity among squares appear most problematic in the Finland survey (Lahti et al. 1997), although all surveys will suffer from these problems to some extent. In the Warwickshire survey, the 2 x 2 km squares were not all searched in their entirety, but at least one quarter of the area of each square was intensively surveyed (Cadbury et al. 1971). These limitations of the data should be considered in the interpretation of results. Table 1 summarizes the characteristics of the nine data sets used in our study, which have quadrat dimensions ranging from 1 x 1 m to 50 x 50 km.

Boundary or coastal grid cells which contained less land area than a complete square were omitted from each survey, as were islands (including Britain for the European data set). Therefore, each data set used in the analysis consisted of a contiguous assemblage of equal-area squares. However, several grid cells in the European data set are of unequal size, since strips of widened or narrowed cells are required in order to fit a grid to the curved surface of the Earth at this scale (23 % of squares affected). These grid

cells range in width from 40 to 60 km rather than the usual 50 km; their height was constant at 50 km. The analysis was performed without attempting to correct for unequal grid cell area since the errors in species lists due to uneven sampling effort are likely to be more important than errors due to unequal area. Eastern Europe was removed from the data set due to inconsistent sampling intensity compared to western Europe.

Taxonomically, the species used in analyses were the Pteropsida or ‘true ferns’; however, the aquatic families Azollaceae, Marsileaceae and Salviniaceae were excluded because the spatial behavior of the aquatic ferns will be subject to extremely different constraints than the terrestrial community.

Null models

Each data set was organized as a matrix containing binary records of presence or absence of species at each site. The column totals represent species richness of each site while the row totals represent the number of occurrences, or range size, of each species. To separate the effects of heterogeneity or structure from pure scale effects, we destroyed portions of the data’s spatial structure by randomizing the data matrix to produce null models of species distributions. Differences in diversity patterns between the reconstituted and real data will reflect the amount of spatial structure inherent in the survey. The complex nature of spatial variation requires the use of several null models which isolate different components of spatial aggregation (see Table 2 and following paragraphs for details). The data matrices were randomized in three ways:

- 1) The spatial location of the quadrats was randomized or “shuffled” to produce the Shuffle model. This procedure destroys the spatial associations between species in different grid squares but preserves within-quadrat species associations. The distribution of species richness and range size are unaffected. A species-area curve from this data is equivalent to one constructed by adding together randomly selected quadrats.

- 2) Species were allocated randomly among sites, with each species retaining its original number of occurrences. Therefore, the number and identity of species within

Table 2. The components of spatial variation of diversity which are destroyed (-) or maintained (+) in each null model.

Model	Spatial aggregation of species	Spatial structure of species richness	Within-hectare species associations
Data	+	+	+
Shuffle	-	-	+
Random	-	-	-
Constrained Random	1/2	+	-

each quadrat changes as co-occurring sets of species are broken up. The distribution of range size is unchanged, but the distribution of species richness becomes much more even, following a Poisson distribution. This model was termed the Random model. There should be a difference between this model and the previous one when the size of the quadrats is large enough so that the spatial structure maintained within quadrats in the Shuffle model produces a noticeable effect on diversity patterns which is destroyed in the Random model.

3) Species were distributed randomly among quadrats with the constraint that both species (row) and site (column) totals in the matrix remain fixed. We refer to this matrix as the Constrained Random model. The frequency distributions of species richness and range size are maintained, as is the spatial structure of species richness. However, the distribution of individual species is not completely random since occurrences are restricted to sites which contain at least one species.

Diversity patterns

The complex arrangement of organisms in space produces a mosaic in which ecologists and biogeographers observe patches, gradients, endemism and hotspots of diversity. The simplest way of representing this variation may be to examine the separate components of variance of the species by sites matrix. We present the frequency distribution of species richness among sites and the distribution of range size or the number of occurrences of each species as a measure of the inherent variation present in each survey.

Species-area curves were constructed from all data sets and from the reconstituted null matrices. Increasingly larger areas were sampled by aggregating adjacent quadrats into larger units (2 x 2 squares, 3 x 3 squares, etc.). This process can be visualized as laying a coarser grid over the original set of quadrats. The average values for all non-overlapping quadrats of each size were used to construct species-area curves in log-log space. This technique produces species-area curves which are equivalent to those

obtained by taking the average of several nested samples of increasing area (Condit et al. 1996). As area of the aggregate quadrats increases, the sample size necessarily decreases; we continued the aggregation process as long as we could obtain at least five replicates (with the exception of four 5 x 5 cell samples for the Duke Forest, which was the maximum possible in the square area of 100 grid cells).

As a measure of similarity of species composition, we calculated the correlation between species presence and absence among each pair of quadrats; we refer to this as the specific correlation between two quadrats. The correlation was calculated according to the following formula:

$$r_s = \frac{Cov_{12}}{s_1 s_2}$$

where Cov_{12} is the binary covariance between the two quadrats, or:

$$Cov_{12} = \frac{n_{11}n_{00} - n_{10}n_{01}}{N(N-1)}$$

where n_{11} , n_{00} indicate the number of matching species (both present or both absent) and n_{10} , n_{01} indicate the number of species which are present only at site 1 and only at site 2, respectively. N is the total number of species in the survey.

For each site, the binary standard deviation of species richness (s_1 and s_2) is calculated by:

$$s = \sqrt{\frac{S(N-S)}{N(N-1)}}$$

where S is the number of species present in the grid square and N is the total number of species in the survey.

We plotted the mean correlation among all pairs of sites in several distance intervals. Correlation values will be positive for pairs of sites with similar species composition, and will be negative if species found at one site tend to be absent at the other. When one or both sites in a pair have zero species, the correlation is equal to zero. The correlation values are affected by species not found in either site, since a species absent at both sites contributes to the calculation in the same way as a species present at both sites. We assume that a species' absence is as important as a species' presence in characterizing similarity among sites. Specific correlation values were calculated only for pairs of sites at a distance of no more than half the maximum distance possible in the data set. This ensures that every quadrat enters into the calculations of averages for every distance interval. If one continues the calculations up to the most distant quadrats, then the quadrats in the center of a region will not contribute to the averages for these larger distances, because they are not far enough away from any other square.

We also plotted the average number of species found at two sites as a function of distance between the sites. If specific correlation values decline with distance, then the species richness of two sites should increase; the rate of increase will reflect the amount of species turnover through space. However, the total number of species found at two sites should reach an asymptote determined by the combined area of two quadrats. If we assume that two adjacent quadrats have very similar or identical species composition, then the asymptote should occur at a species diversity of double the average diversity for adjacent squares, when the two squares have completely different species composition. Despite this inherent non-linearity, the initial increase phase of the curve provides a useful measure of species turnover, and the distance at which the curve levels off is also interesting.

The specific correlation and the number of species found at two sites are only two possible ways of quantifying the similarity of species composition between pairs of sites. Other possible indices include the familiar beta-diversity (Whittaker 1972), complementarity (Colwell and Coddington 1994) or more complex ordination techniques (Legendre and Legendre 1983). We chose to employ relatively simple measures in this

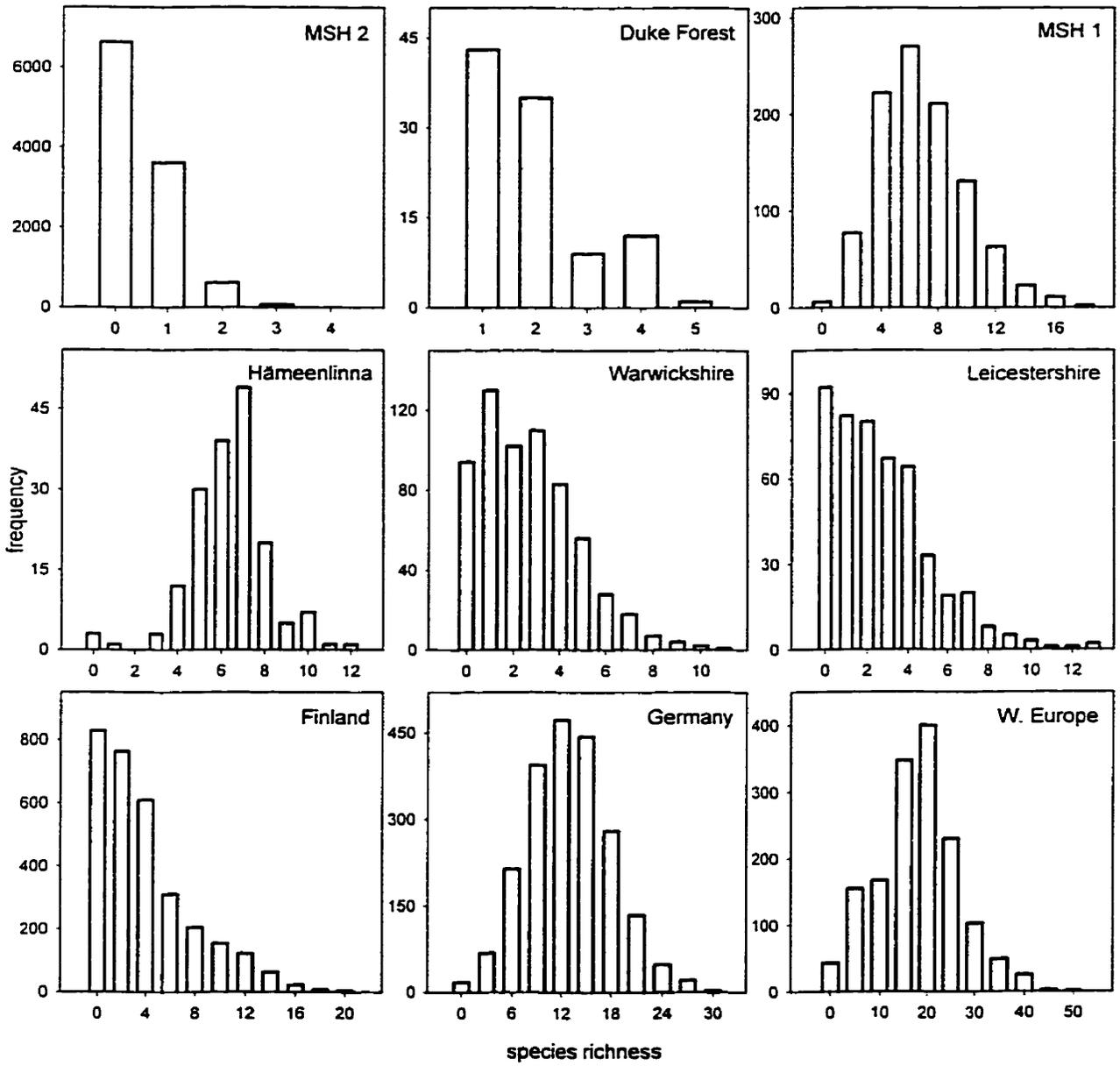
study since their spatial and statistical behavior can be more readily visualized and interpreted.

Results

Variation among species and among sites

The distribution of species richness varies in shape among the different data sets. It is strongly right-skewed for MSH 2, for the Duke Forest and for Finland (Fig. 1). A right skew may be likely for any data set with low average diversity per grid square, since the number of species is constrained on the left to a minimum value of zero while the right end of the distribution can theoretically extend outwards up to a maximum set by the total number of species in the region. Consequently, we expect a right-skewed distribution for surveys in which each grid square is very small, since the sites will contain few individuals or few different habitats and therefore few species. This pattern is observed for the MSH 2 survey, in which 94 % of the 1 m² grid squares contain zero or one species. In general, one might expect that as the area of grid squares increases, average diversity will rise and the distribution should be drawn out towards the right, becoming arithmetic-normal. However, there is no consistent tendency for larger-scale surveys to have more normal distributions in this study. Quite the opposite occurs for Finland, which has a strongly right-skewed distribution despite a grid square area of 100 km². In this case, the low average diversity per square must be attributable to other factors such as low productivity levels or low or irregular sampling effort. The other large-scale surveys of Germany and Europe do have very symmetrical distributions of species richness, but then so does the much smaller Hämeenlinna survey. The other three data sets, Warwickshire, Leicestershire and MSH 1, have intermediate, slightly right-skewed distributions. The distribution of range size, or the relative frequency of occurrence of each species, is very strongly right-skewed on arithmetic axes: within each survey, most species are relatively uncommon. When expressed on a logarithmic axis, the

Figure 1. Frequency distributions of the number of fern species per quadrat. Note that the number and size of quadrats varies among surveys; see Table 1 for details.



distributions of range size are roughly normal to somewhat left-skewed and are fairly similar across all scales (Fig. 2).

The variance of species richness among sites is much lower than the variance of abundance or range size of species. This pattern may have a simple cause: the maximum number of species at a site cannot exceed the total number of species for the region, whereas the number of occurrences of a species can range between one and the total number of grid squares, which is determined by the sample design and is much greater than the number of species in all these surveys. Moreover, in every survey the variance in species richness among sites is higher for real data than for the Random model of completely uncorrelated species distributions, suggesting that there are positive associations among species which tend to congregate in diversity "hotspots" (Palmer and van der Maarel 1995).

Comparison of data and null models

Species-area curves are linear or slightly convex on log-log axes (Fig. 3). In five of the data sets (MSH 2, MSH 1, Finland, Germany and W. Europe) the randomized data lie well above the real data, indicating a substantial effect of spatial structure. The within-hectare species associations maintained in the Shuffle model do not affect the curve compared to a random assortment of species, as there is no difference between the Random and the Shuffle curves. The Constrained Random curve falls between the data and the other random models, reflecting the limitations of this randomization: it is not possible to completely destroy spatial structure in the data while maintaining the row and column totals constant. Compared to the first five data sets, there is little difference between the data and null models in the four remaining surveys. The Random and Shuffle models lie fairly consistently above the data for the two British counties, but the Constrained Random model is indistinguishable from the data. For the Duke Forest and Hämeenlinna, the four curves are not clearly separate. It is important to remember that the curves in Figure 1 do not extend to the total area of each survey, at which point all the curves would converge. The range of area displayed for each curve represents the

Figure 2. Frequency distributions of the range size or number of quadrats occupied by each fern species. Range sizes were converted to relative frequencies and then log-transformed.

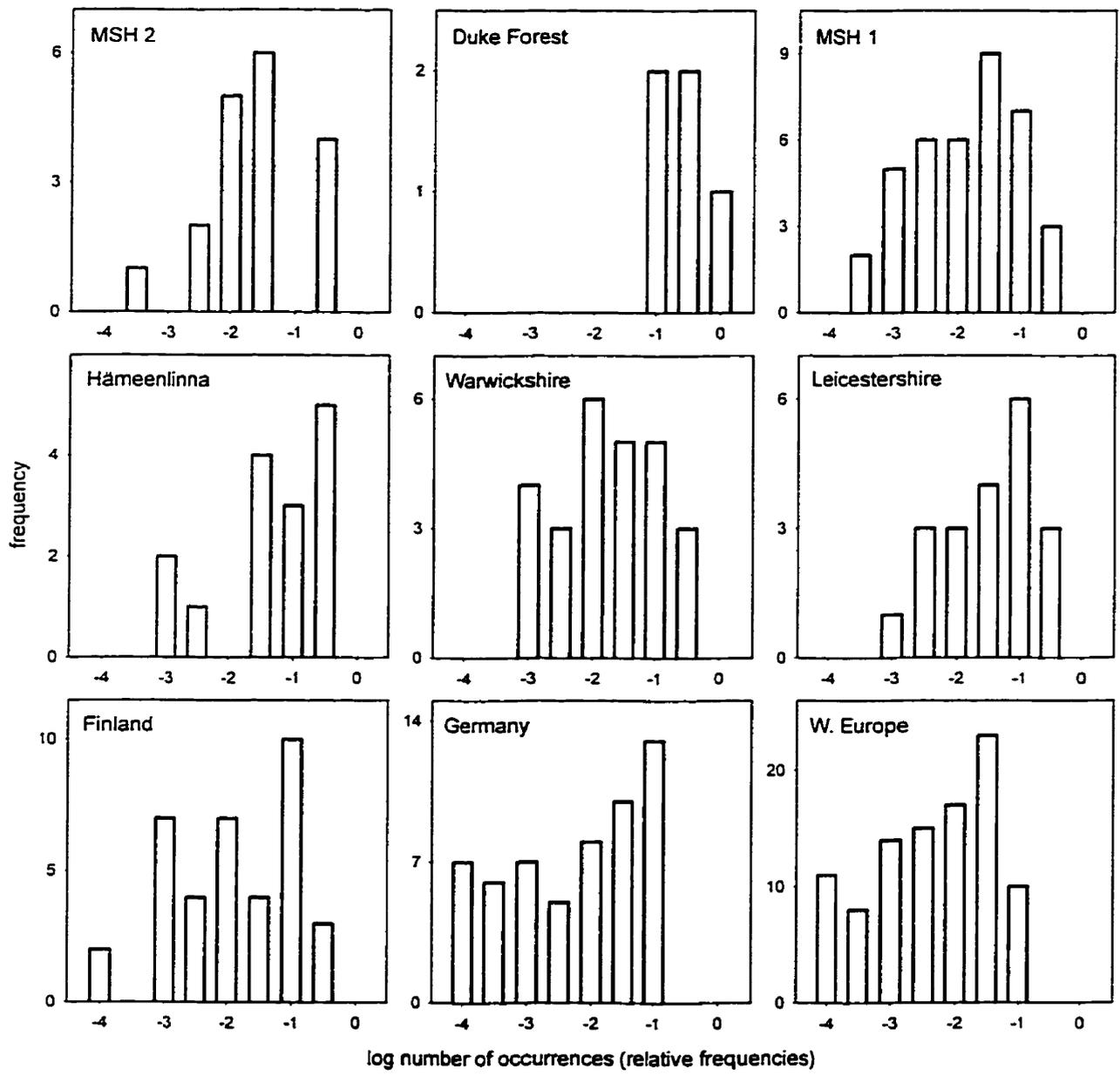
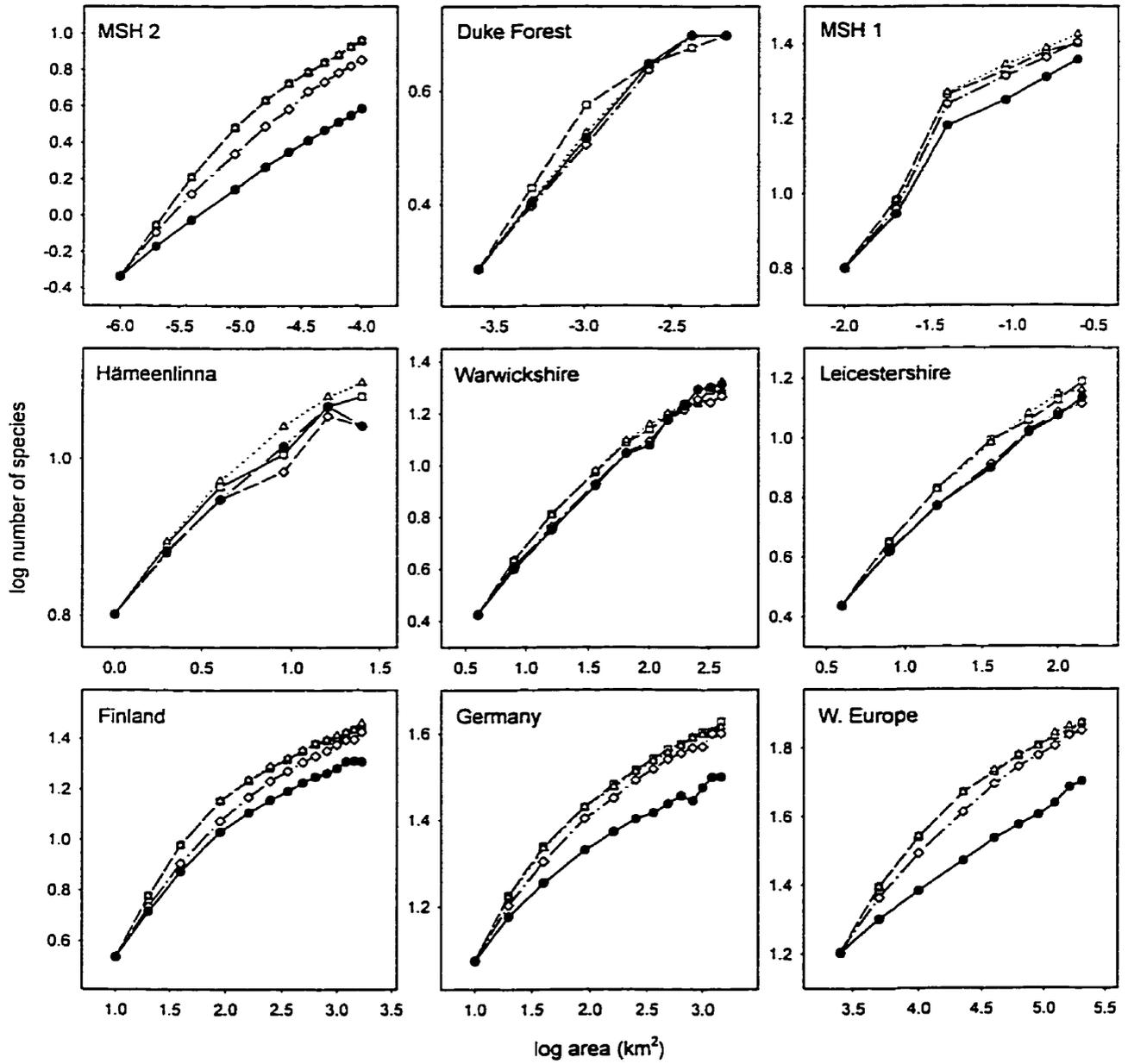


Figure 3. Species-area curves for data and three null models of random species distributions. Each point represents the average species richness of five or more non-overlapping samples of each size. Circles/solid line: data; squares/dashed line: Shuffle; triangles/dotted line: Random; diamonds/dot-dash: Constrained Random.



proportion of the total area which could be represented by at least five non-overlapping aggregate samples. This proportion is dependent on the region's shape, so the range of area does not represent the same percentage of total area in each case. The irregular oscillations at the right end of some curves seem likely to be the result of small sample sizes for these areas.

The specific correlation between pairs of sites decreases nearly linearly with distance for most data sets (Fig. 4). However, the decrease in correlation becomes steeper at large distances for Warwickshire and W. Europe whereas the Duke Forest and MSH 1 show a slower rate of decline at large distances. The curves for the Random and Shuffle null models are both flat since in these models there is no difference on average between sites which are close together and sites which are far apart. In certain cases these two curves occur at different elevations, indicating a different overall average correlation between grid squares. The largest difference occurs for Finland, which has a very low average correlation among quadrats in the Shuffle model, due to its very skewed distribution of species richness. The Random model allocates species much more evenly among quadrats, producing a higher overall correlation.

The average number of species in two sites initially increases nearly linearly but then undergoes a sharp decline at the right end of all curves except MSH 2 (Fig. 5). This drop in species number occurs at a diversity level less than double the species richness of adjacent pairs of squares, and is not paralleled by a corresponding increase in correlation values at that distance. Once again, the Shuffle and Random models are both flat, and the Constrained Random model lies in an intermediate position between the data and the other random models. As observed for the species-area curves, the patterns for correlation-distance and species-distance relationships for the Duke Forest, Hämeenlinna, Warwickshire and Leicestershire are noisier and less distinctive, although the same general trends emerge.

Figure 4. Average specific correlation between pairs of quadrats as a function of distance.
Circles/solid line: data; squares/dashed line: Shuffle; triangles/dotted line:
Random; diamonds/dot-dash: Constrained Random.

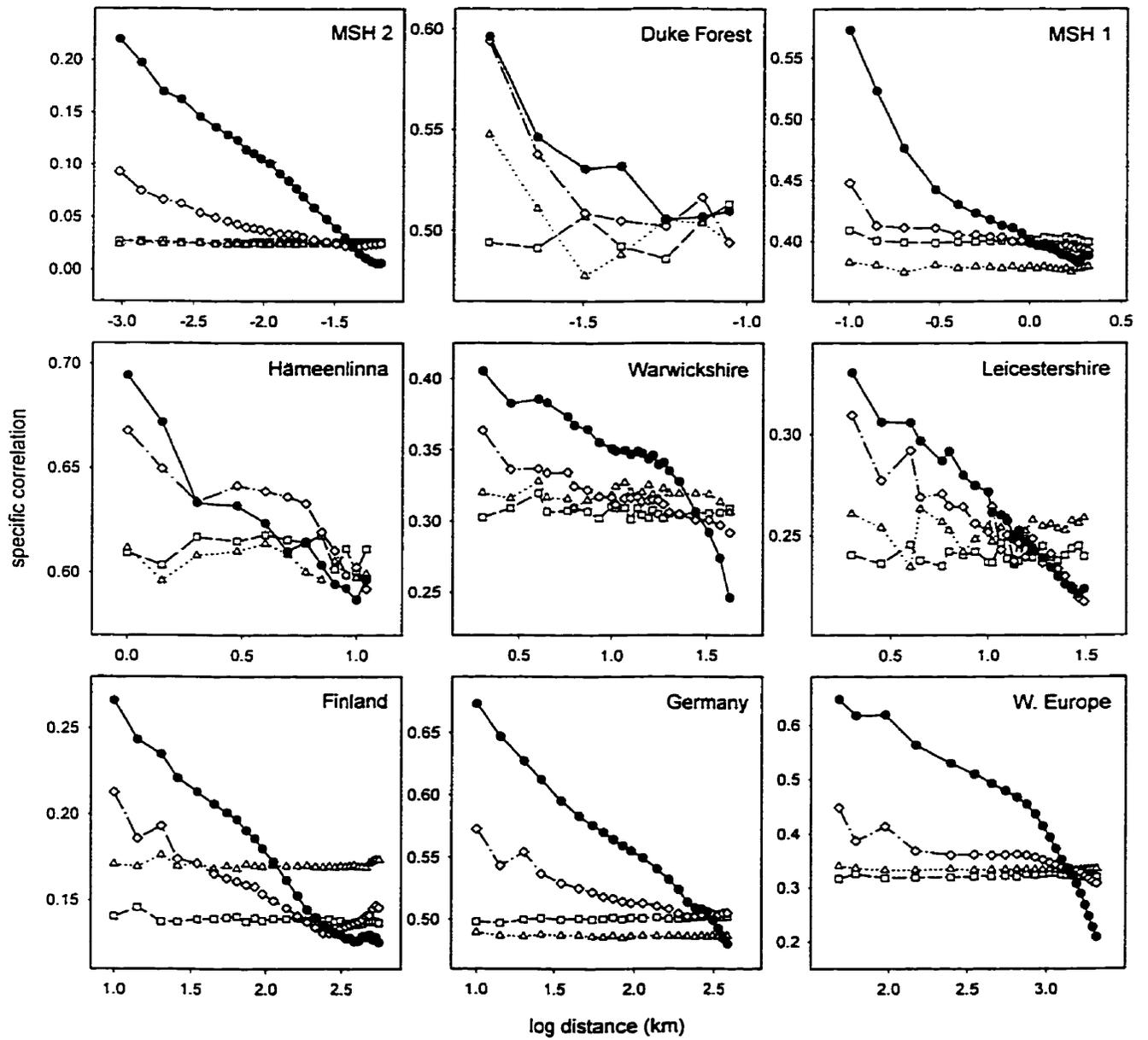
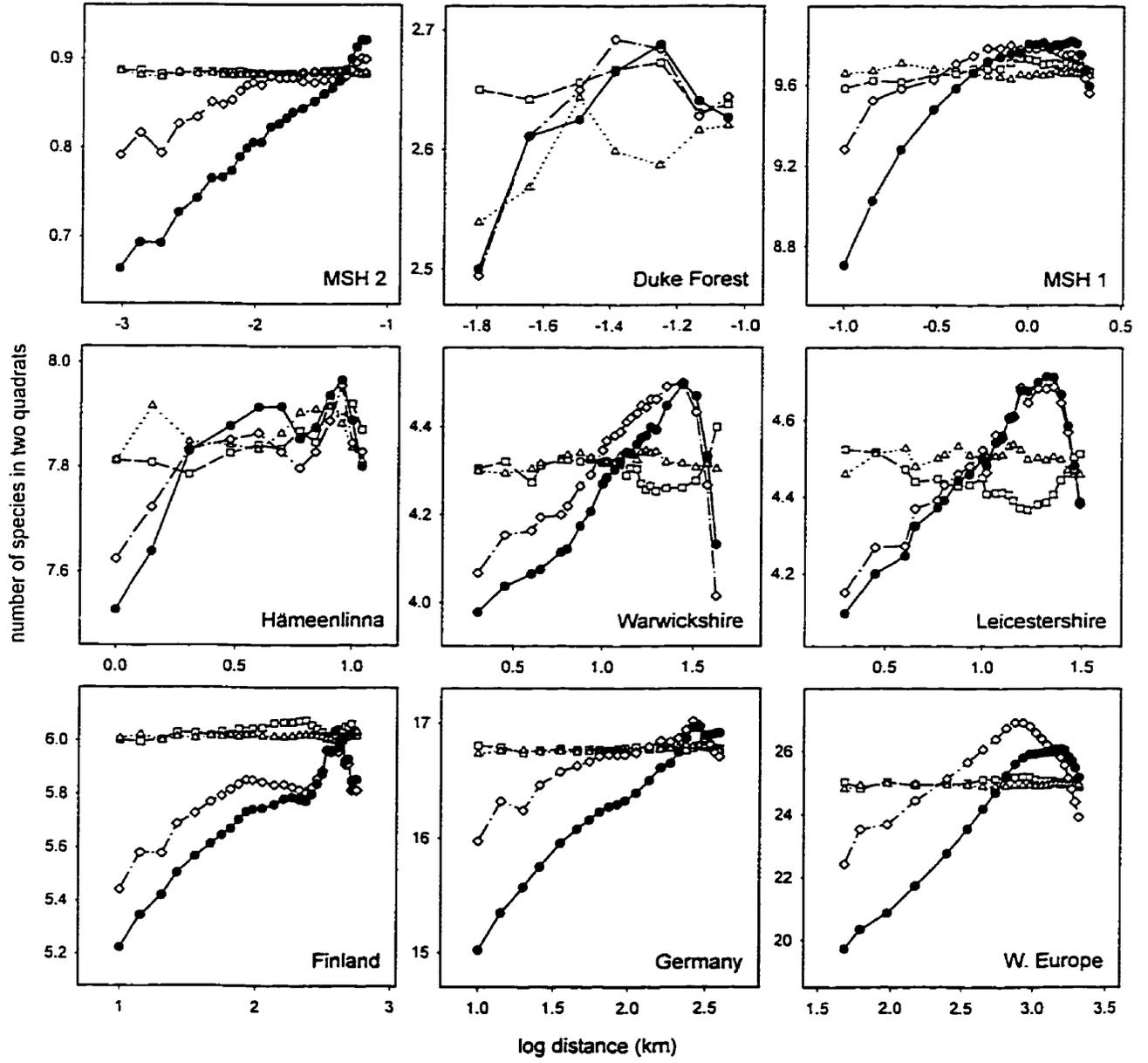


Figure 5. Average number of species in a pair of quadrats as a function of distance.
Circles/solid line: data; squares/dashed line: Shuffle; triangles/dotted line:
Random; diamonds/dot-dash: Constrained Random.



Cross-scale comparison

The species-area curves for all surveys are compared in Figure 6. These curves include the total area of the survey, and have slopes ranging between 0.16-0.44 (Table 3). These slope values are typical of those reported for a variety of taxa and scales (May 1975, Connor and McCoy 1979, Rosenzweig 1995). The addition of the total area to the initial curves generally produces a very slight downward curvature, except for the Duke Forest which has more pronounced non-linearity. The steepest slopes occur in Warwickshire, Leicestershire and MSH 2, while the shallowest slopes are observed for Hämeenlinna and Germany; there does not appear to be any consistent change in slope value in relation to spatial scale. However, elevation of the curve is negatively related to quadrat size for the nine surveys ($p = 0.005$, $r^2 = 0.70$). The species-area relationship connecting all the total areas is shallower than any of the individual curves (slope = 0.10). An interesting separation appears between the North American and the European data sets, in which the North American curves seem to lie along a line of overall higher species richness than the European curves. This separation contributes to producing the shallow slope of the line connecting all areas. However, the pattern remains but is less pronounced if only the European data sets are included (slope of total areas = 0.19).

The curves of specific correlation as a function of distance have remarkably similar slopes among the different surveys (-0.08 to -0.12) with the exception of the European survey, which has a steeper slope of -0.25 (Table 3). The European curve is non-linear and declines most rapidly at distances greater than about 600 km (Fig. 7). Average correlation values do not become negative at any scale, as species which are absent from both sites being compared tend to keep the correlation values positive or near zero despite increasingly different species composition with distance. The effect of species absent from both sites is reflected in the curve's elevation, which appears to be related to the distribution of species richness rather than spatial scale. In surveys with right-skewed distributions of species richness, the entire curve is drawn towards zero by sites without any species (zero sites) in addition to numerous species absent from both sites. Thus, the elevations of the curve for Hämeenlinna, Germany and Europe are high,

Figure 6. Cross-scale comparison of species-area curves. Larger, cross-hatched symbols represent the total area of each survey; the solid line is the species-area curve for the total areas.

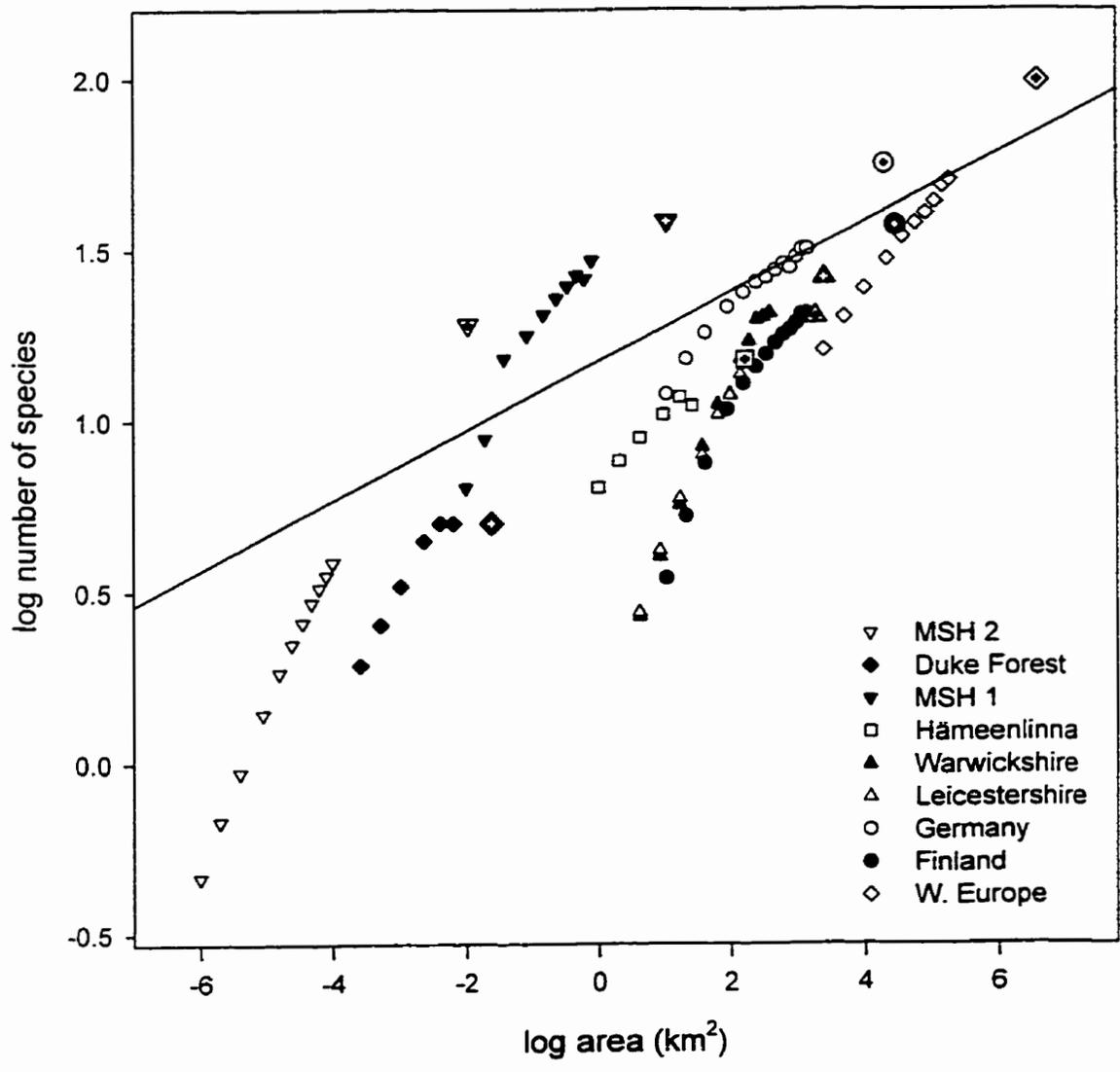
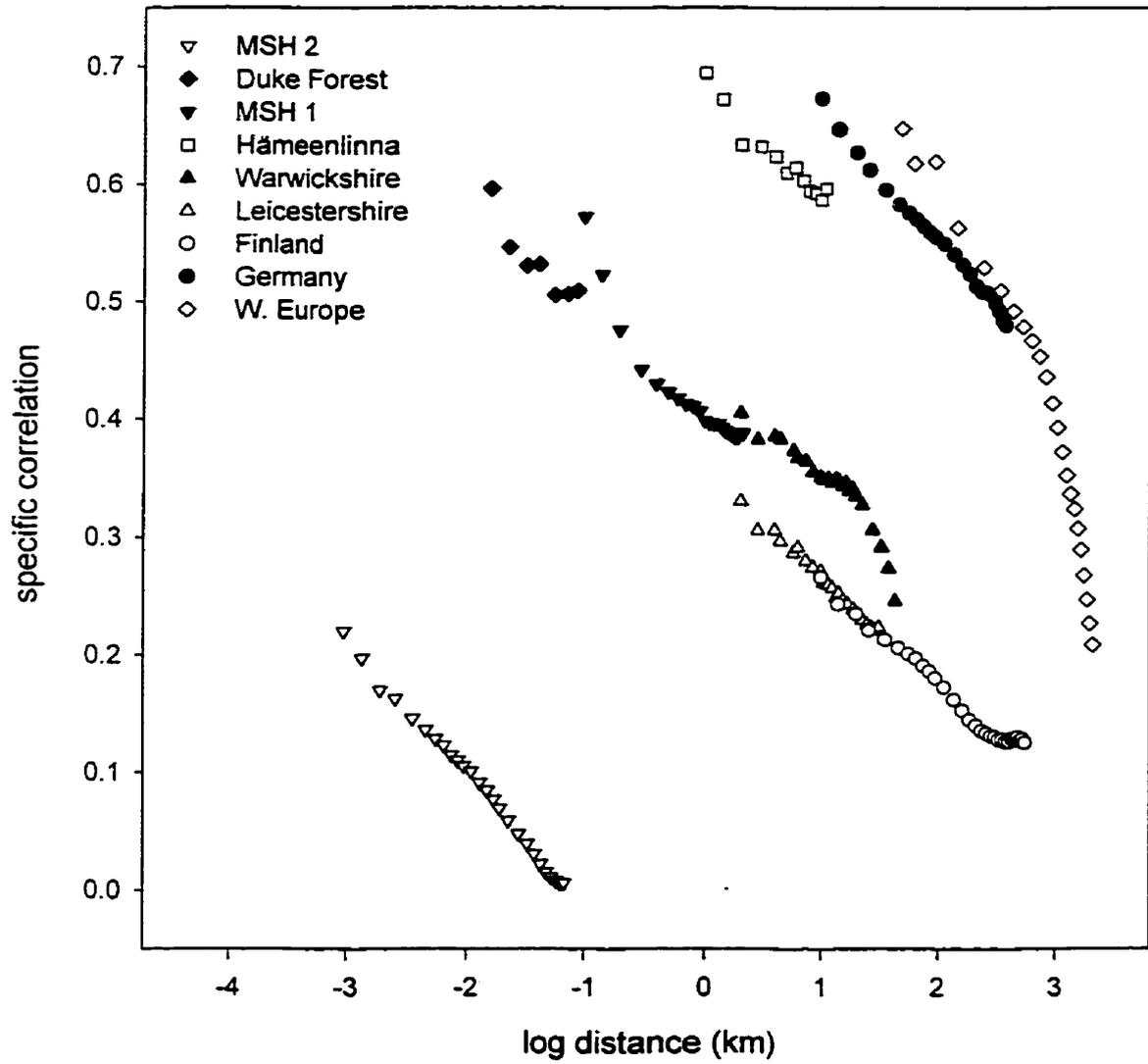


Table 3. Cross-scale comparison of slope (z) values for the relationships between species number and area ($\log S:\log A$); specific correlation between two sites and distance ($\text{Corr}:\log D$); and the number of species at two sites and distance ($S:\log D$; $\log S:\log D$).

Data set	$z[\log S:\log A]$	$z[\text{Corr}:\log D]$	$z[S:\log D]$	$z[\log S:\log D]$
MSH 2	0.40	-0.11	0.13	0.07
Duke Forest	0.20	-0.11	0.16	0.03
MSH 1	0.26	-0.12	0.64	0.03
Hämeenlinna	0.16	-0.09	0.28	0.02
Warwickshire	0.38	-0.10	0.35	0.04
Leicestershire	0.44	-0.09	0.43	0.04
Finland	0.29	-0.08	0.36	0.03
Germany	0.19	-0.11	1.14	0.03
W. Europe	0.24	-0.25	3.96	0.07

Figure 7. Cross-scale comparison of the decline in specific correlation between pairs of quadrats as a function of distance.



whereas Finland and the British counties are lower, and MSH 2 is the lowest. The Duke Forest curve remains high despite a right-skewed distribution of species richness since the mean square richness of 1.93 is close to the total number of species in the region (five). To examine the effect of zero sites on the curves, we recalculated correlation values excluding all sites with species richness of zero from comparisons. For Germany, Europe, Hämeenlinna, MSH 1 and the Duke Forest there was little change in the curves since these surveys have few zero sites. The elevation of the curves increased slightly for Finland, Leicestershire and Warwickshire as a result of removing many zeroes from each distance interval, but the slope changed very little. Only the MSH 2 curve had a dramatic change in slope (from 0.1 to 0.43) when the zero sites were removed, because the left end of the curve shifted upwards while the right end of the curve did not change; there was no effect of removing zeroes since the average correlation was already zero. Despite the impact of these sites on the slope of MSH 2, we have chosen to retain the sites without species in the analysis. The zero sites are interspersed and not obviously different from adjacent sites which do support species; they are mainly a result of the fine resolution of the survey. When meter quadrats are aggregated into larger 10 x 10 m units, the distribution of species richness becomes symmetrical with hardly any zero sites.

The number of species in two sites as a function of distance seems to increase more rapidly in the large-scale surveys. The steepest curve is for Europe while the shallowest is for MSH 2 (Table 3). As explained previously, the average number of species in adjacent squares is constrained by the area of the squares. The curve should increase to a level of no more than double the initial richness of pairs of adjacent squares. At larger scales, this increase will be greater in absolute terms, for example from 15 to 30 species, while at very small scales, the increase may be constrained to a doubling from 1 to 2 species, producing the general trend towards steeper slopes at large scales. If species richness is expressed logarithmically, then the slopes are all very similar, but all near zero (0.02-0.07) since the increase in species number is so small (Table 3). The curves are not illustrated together on one graph since their different elevations are dependent on the limitations to species richness imposed by the area of a quadrat. The most useful comparisons of elevation are thus between surveys conducted on the same scale (ex.

Finland and Germany). In this case the difference in elevation is a function of the difference in average diversity levels between the two regions, and as such is related to the form of the distribution of species richness, either right-skewed or symmetrical.

Discussion

Multiple dimensions of spatial structure

Spatial heterogeneity is a functional force in maintaining biological diversity, both at the genetic level, through local adaptation if dispersal rates among patches are low (the 'Tangled Bank' theory in Bell 1982, Hedrick 1986), and at the species level, through the coexistence of specialist species in different patches (Tilman and Pacala 1993). Given its considerable importance, we expect to observe the contribution of spatial structure to diversity patterns over and above the ubiquitous effects of scale. Our technique of comparing survey data to null models does in fact allow us to demonstrate the consequences of spatial structure for diversity patterns. As expected, specific correlation values decrease with distance and the number of species at two sites increases with distance, whereas the curves for null models are flat. Moreover, real species-area curves increase less steeply than those for random data as a result of spatial structure.

The behavior of the different null models reveals the complex nature of spatial variation: diversity patterns are influenced by the spatial arrangement, diversity and composition of sites as well as the distribution of each species. The Random and Shuffle models produce nearly identical species-area curves and species-distance curves, since individual species are randomly distributed in both these null models. However, differences between the two models appear in the correlation-distance curves, where the exact species composition becomes relevant. In the Shuffle model, the species composition of each quadrat is exactly the same as for the real data, while in the Random model species composition is completely unpredictable. The largest difference between the two null models is observed in the Finnish survey due to the very high number of grid

cells with zero species. The resultant high proportion of pairwise comparisons in which one or both sites have no species produces a very low average correlation in comparison to the Random model, which has the same number of species per quadrat on average but has ten times fewer empty quadrats. The same large difference in correlation values does not occur for MSH 2, despite its highly skewed distribution of species richness, because the quadrats in the survey are so small that over 90 % of sites contain only zero or one species in both the Random and the Shuffle models.

The effects of scale and structure cannot be entirely separated in the Constrained Random model, which invariably remains closer to the data than the other two random models. This result indicates that the spatial structure of species richness itself contributes to diversity patterns, regardless of the actual species composition at each site. The important influence of the distribution of high and low diversity patches is particularly apparent for Warwickshire and Leicestershire which have indistinguishable species-area curves for the data and Constrained Random models (Fig. 3). We examined the distribution maps of species richness for each of these counties and found that in both cases the highest-diversity quadrats cluster in a single small area, with no other equally rich sites elsewhere. The rate of accumulation of species with area is largely dependent on these single patches of richness, and consequently we observe nearly identical curves for the data and the Constrained Random model, which both retain the spatial structure of diversity.

The most striking differences between the data and null model curves seem to occur at the very small scale of one hectare (MSH 2) and the very large scales of Finland, Germany and Europe. The curves for MSH 1 are also relatively distinctive, but the four other data sets exhibit only small or non-detectable differences among species-area curves and more noisy patterns generally. It is possible that spatial heterogeneity among quadrats is maximal at very small and at very large scales, producing the major differences among curves. However, it seems more likely that the results are affected by the number of quadrats in a data set, not just their size. The five surveys with the largest differences between the curves all contain over 1000 grid squares, while the Duke Forest,

Hämeenlinna, Warwickshire and Leicestershire surveys contain fewer than 650 quadrats. Sampling a larger number of quadrats within a region, effectively increasing the resolution of a survey, should increase the variance among squares and decrease the variance within squares of a composite variable such as species richness. Therefore, a stronger overall effect of structure is observed in the diversity data when sample size is increased.

Spatial variation of species composition

Characterizing the change in species composition from place to place is at least as important as the change in species number with area (Colwell and Coddington 1994). The degree of species turnover through space will determine overall regional diversity levels, and the structure of species distributions will influence processes such as competition and trophic interactions. The quantification of species turnover should prove useful in improving the predictive ability of spatial models and of techniques which seek to estimate diversity by extrapolation (Palmer 1990, Colwell and Coddington 1994, Harte and Kinzig 1997).

Although several analyses have addressed the level of environmental variance across scales (Robertson et al. 1988, Lechowicz and Bell 1991, Bell et al. 1993), few studies have examined the spatial structure of community composition over a very broad range of scale (but see Böhning-Gaese 1997 for birds). We have observed remarkably consistent rates of change in fern species composition with distance at very different spatial scales. The similar slopes of the correlation-distance curves (Table 3) suggest there are similar levels of spatial structure among quadrats at all scales, perhaps reflecting the relatively similar distributions of range size in all these surveys (Fig. 2). The log-normal distribution of range size appears to be the norm for most taxa at most scales (Gaston 1994b, Gaston 1996). This distribution may be related to the commonly observed log-normal distribution of abundance among species (Preston 1962, May 1975), since at very fine sampling scales, the distribution of range size approximates the distribution of abundance. The average size, aggregation and degree of nestedness of species ranges will

affect the rate at which species composition changes with distance. We may expect higher slopes for correlation-distance and species-distance curves if average species ranges are small, as they generally are in tropical locations (Stevens 1989). We would also expect steeper curves for taxa with lower dispersal ability than ferns, such as large-seeded plants. Harrison et al. (1992) did not observe higher species turnover for taxa with lower dispersal rates along two transects in Britain, but it would be worth pursuing a broader examination of this pattern over a range of geographical areas and scales.

The lack of breakpoints or thresholds in the correlation-distance curves does not support the view that ecological patterns are hierarchical (Kotliar and Wiens 1990), but rather that patterns change in a continuous fashion across scales (Palmer and White 1994). The most prominent exception is for Europe, in which we seem to see evidence of a threshold: above a distance of around 600 km, the specific correlation values decrease more rapidly. At these large distances, we may have moved beyond the limits of most species ranges, combining pairs of sites from regions with separate biogeographic histories. Other shifts in slope, such as that observed for Warwickshire and certain upward curving lines may result from spatial structures of diversity particular to those surveys. Unlike the correlation curves, the number of species in two quadrats undergoes a definite decline at large distances in nearly all data sets, suggesting that a characteristic distance between high diversity patches exists in each region. Extreme aggregation of high diversity sites into a single general area is probably behind the most precipitous declines which occur for Warwickshire and Leicestershire at distances greater than 20 to 25 km.

Species-area curves across scale

Why should the species-area curve connecting the complete regions be shallower than the individual curves within each survey? The sampling of a similar-sized area at a finer scale will usually result in a longer species list. For example, our intensive census of one hectare at Mont St. Hilaire (MSH 2) found 19 species (Richard et al. in prep.), compared with a mean value of 6 and a maximum of 18 species found among all hectares

of the mountain for MSH 1 (Bell and Bernhardt in prep.). The higher species number observed for the same area causes the smaller-scale curves to be shifted upwards, producing the negative relationship between elevation of the species-area curves and area of one quadrat. Moreover, the smaller surveys are all shifted towards the left of the area axis; combined with their higher elevation, the left-hand position contributes to the shallow slope among all areas. In their exploration of the effect of scale on the Duke Forest data, Palmer and White (1994) observed a set of parallel curves at different scales, connected along the bottom by a shallower slope. In their case, the shallower slope represents a nested species-area curve from the same data as the other curves which were created from disaggregated quadrats.

The separation between the three North American curves and the European curves seems to suggest an overall higher level of fern diversity in North America and also contributes to producing the shallow slope connecting the surveys. However, other factors besides continental location also differ between these two sets of curves: the North American data sets are the smallest-scale surveys, they are completely forested and relatively undisturbed. Any of these differences may influence the species-area curve and cannot be distinguished based on our data.

Conclusions

The current worldwide knowledge of diversity patterns is uneven and incomplete. Many people are advocating intensive surveys of species and genetic resources, in order to learn as much as possible before it is too late (Colwell and Coddington 1994). Effective surveys must rely on better characterization of species distributions, if we hope to estimate and predict diversity in poorly-known areas. The quantification of species turnover in space and time will also be useful in the development and testing of ecological and evolutionary theories and models. Our technique of comparison to null models allows us to isolate the effects of structure on diversity patterns, and provides a potentially useful measure of the degree of species turnover. However, the complexity of diversity patterns remains difficult to describe with any one simple expression, which

raises questions about the utility of single indices for characterizing diversity (Magurran 1988).

A complete analysis of diversity patterns should include all dimensions of the species by site matrix, in order to achieve a more precise understanding of the nature of variation and the effects of interactions between species and sites. For binary data, the relevant parameters are species richness and range size, while for quantitative data we can also include the total number of organisms at a site and the total number of individuals of each species. Some of these parameters, such as relative abundance, have been studied much more extensively than others; however, all dimensions of variation should be integrated into a complete description of diversity data. The distribution of species richness in particular is only rarely reported, although the variance has been considered in the context of community saturation or niche limitation (Wilson et al. 1987, Palmer and van der Maarel 1995). We found evidence that both the spatial structure of diversity in the landscape, and the right-skewed or symmetrical form of its distribution among sites, have important implications for the more familiar patterns of species accumulation with area and species turnover from place to place.

We have observed similar species diversity patterns in fern communities at several scales, suggesting that similar levels of spatial heterogeneity exist across this broad range of scales. Further exploration should focus on the form of species-area, correlation-distance and species-distance curves across spatial scales for other taxa with different dispersal properties and habitat requirements than the ferns. Ultimately, species distribution patterns should be related to variation in environmental factors, to examine whether diversity can be related to the spatial structure of environmental variables at different spatial scales.

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Summary

Spatial heterogeneity is functional in ecosystems: it contributes to the maintenance of both genetic diversity and species diversity (Legendre and Fortin 1987, Bell 1982). The general objective of this thesis was to study diversity patterns and their relationship with environmental heterogeneity. The environment is patchy and structured, even at very small scales (Robertson 1988, Lechowicz and Bell 1991). One theory for the maintenance of diversity holds that, through the processes of selection, different species should adapt and specialize to a particular set of environmental conditions in which they can maintain higher relative to other species. If selection is the most important force determining species spatial distributions we should observe a positive relationship between diversity and the environmental variance within sites. This relationship has previously been established for fern species diversity in an extensive survey of more than a thousand one-hectare quadrats (Bell and Bernhardt in prep.). In Chapter 1, I tested whether a similar relationship between fern species distributions and environmental structure existed at scales smaller than one hectare. Ferns were used for these studies since their mode of reproduction by spores suggests their distribution should be predominantly influenced by environmental conditions rather than dispersal limitations (Peck et al. 1991). In Chapter 2, I compared the local, small-scale diversity patterns of these two studies to other surveys covering a very broad range of scale. The contribution of spatial structure to species-area curves and to the decrease in species correlation of sites with distance were examined by comparison to null models of random distribution.

The patterns we observed at small scales in Chapter 1 indicated that species as well as soil conditions and physical features are spatially structured within one hectare of old-growth forest. Fern species are distributed in different parts of the hectare: some species are restricted to the wet area, others are restricted to the slope. Based on the similarity of their spatial distributions, species were divided into groups, however, species within a group did not always share very similar soil preferences. The number of species at two sites increased with distance between the sites, as the composition of sites became more different with distance. The variance of species diversity among sites is much

higher than expected from a random distribution, such that species are relatively aggregated into hotspots of diversity as opposed to a more even distribution among sites. Diversity was highest at sites with high soil moisture and/or low soil fertility. However, despite the evident spatial structure of species distributions and of environmental conditions, there was no relationship between diversity and within-site environmental variance. Our measure of spatial heterogeneity may not correspond to the scale of the ferns' functional heterogeneity (Kolasa and Rollo 1991). The dispersal of spores away from the parent plant and the immigration of individuals from outside areas will tend to oppose the forces of selection and adaptation, sending propagules into a variety of patch types to which they are poorly adapted. At small scales, the influence of dispersal and immigration may be relatively stronger than selection forces, such that the effect of selection only appears at scales larger than 1 ha. For organisms with lower dispersal capabilities, the scale at which the effect of selection appears may be smaller since less flow of individuals between patches will occur.

The species diversity patterns observed at a local scale were compared to several surveys conducted at larger scales, including the 1 ha scale of Bell and Bernhardt's study (in prep.). The comparison of diversity patterns to null models indicated that spatial structure is present at every scale and contributes to the form of species-area curves beyond the basic effect of increased sampling. The correlation of species composition between two sites also decreases with distance at every scale. The relatively constant slopes of species-area curves and correlation-distance curves indicate that similar amounts of heterogeneity exists across scale, suggesting a fractal process (Palmer 1988, Williamson and Lawton 1991). The frequency distribution of range sizes is relatively constant across scales, but the shape of the distribution of diversity among sites is very different among studies, reflecting differences of sampling scale and sampling effort.

Spatial scale has emerged as a fundamental organizing concept for ecological studies. Patterns of species distributions and diversity change as a function of spatial scale (Palmer and White 1994), as does the relative importance of the processes behind the patterns (Auerbach and Shmida 1987, Kolasa and Rollo 1991). In the two chapters of this

thesis, I compared diversity patterns such as the species-area curve and the change in species composition with distance, and observed remarkable regularities across scale. Environmental heterogeneity is thought to have important effects on species distribution patterns at every scale. However, in Chapter 1, we did not observe an effect of environmental heterogeneity on diversity at a very small scale, although a relationship was observed by Bell and Bernhardt (in prep.) at slightly larger scales. Further work will examine intermediate scales for a relationship, and also compare patterns among groups of organisms with different dispersal abilities. The type of comparative analysis of variance conducted in this study provides a useful approach for examining diversity patterns for different systems and at different scales. By incorporating information on spatial distributions with species traits such as measured environmental preferences, dispersal ability and phylogeny, we can test for the importance of different processes on the creation, maintenance and distribution of diversity at different scales. The establishment of a quantitative and empirical basis for diversity patterns will be a step toward a more complete understanding of one of the fundamental questions of biology.

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