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

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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 metre-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 were formed with species 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 this fine scale.

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A number of ecologically equivalent species can exist in the same place if environmental heterogeneity prevents a single 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 the number of species 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 difficulty inherent in such studies is that the "habitat" is

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a subjective, simplified categorisation of environmental conditions. This classification is useful and quite convenient when comparing sites as different as a meadow and a pond; however, environments are not homogeneous even at very fine 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). Precise boundaries between distinctive habitats or communities rarely exist; rather, there tends to be 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). In order to establish a firm empirical foundation for the relationship between diversity and spatial heterogeneity, it would be helpful to develop straightforward and quantitative measurements

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of environmental variation. This variation may be studied by using several spatially localized measures of environmental conditions (e.g. Bell and Lechowicz 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. 2000).

Bell and Bernhardt (unpubl.) have analysed 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 diversity was greatest in hectares characterised by high soil moisture, low solar radiation and low slope; together these three variables accounted for 22% of the variance of species diversity among hectares. Species diversity was also positively related to the environmental variance within hectares, independently of the effect of the average conditions of growth. 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 diversity, 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). In this paper, we use "small-scale" to mean a fine-resolution survey, while a large-scale refers to a broad or coarse-resolution survey which is often, but not always, conducted over a larger total area. 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 and permits a very detailed exploration of the species' spatial distribution patterns. In the analyses which follow, we examine the variance of diversity among sites, the change in species composition between two sites with distance, 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 at scales ranging from 5×5 to 25×25 m quadrats.

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 by 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. 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 centre 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 10926 quadrats rather than 10000. 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 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 the path, mud, and water only occur in the flat south-west corner. Wood, stumps and tip-up mounds (not shown on the 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 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 the 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 2 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 d 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 h, 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. 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 with a spectrophotometer on days 5, 10 and 15 after inoculation. 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).



Fig. 1. Physical features within the study hectare: rock (grey), path (red), mud (orange), water (blue). The variation in colour intensity from light to dark indicates 0-100% cover of each square meter.

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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 plotted the average variance of pairs of sites as a function of their distance apart (Bell et al. 1993). The slopes of variance plots with logarithmic axes can be compared among variables, with a steeper slope indicating a more coarsegrained 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 25×25 m. These aggregate quadrats were used to construct a speciesarea 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). In discussing results of these analyses, the width of quadrats is used to refer to the scale or size of aggregate quadrats; for example, a 10 m scale refers to the 10×10 m sampling resolution.

To express the degree of spatial dispersion of each species, we use a generalised 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. unpubl.). 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 m² quadrats. As quadrat size increases, the proportion of occupied quadrats, m_L , also increases while u_L decreases. For example, a randomly-distributed species that occupied 30/100 quadrats if the quadrat area is

doubled to 2 m². More generally, the frequency of unoccupied quadrats will decrease following $u_L = e_1^{-Lm}$ 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:

$$(1/\mathbf{u}_{\mathrm{L}})\,\mathrm{d}\mathbf{u}_{\mathrm{L}}/\mathrm{d}\mathbf{L} = -\,\mathrm{c}\mathbf{m}_{\mathrm{L}}$$

Therefore, $-cm_1$ 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 $V_e =$ $\Sigma p_i(1-p_i)$, 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 each of the others. To obtain the mean number of pair-wise combinations expected by chance, the original data matrix was again randomised 10000 times, by assigning species randomly to sites with each species maintaining its original abundance. 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 40/400 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

Table 1. Abundance and dispersion of the 19 fern species recorded in the hectare. R is the number of 1 m^2 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 spatial dispersion with lower values indicating a greater degree of aggregation.

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

composition of two sites as the distance between them increases. A correlation of species composition between each pair of quadrats was calculated using the following formula:

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

where Cov_{12} is the binary covariance between the two sites calculated using presence and absence values of all 19 species and s₁, s₂ are binary standard deviations for each site whose values are a function of the number of species at that site. The value of r_s can range between +1 for two sites with identical species composition and -1 for completely contrasting species composition. 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:

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 $\sigma_{\rm E} = (\sigma_{\rm ms} \sigma_{\rm fy} \dot{\sigma}_{\rm pH})^{1/3}$

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 with a fair degree of caution (Legendre and Fortin 1989); 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 onehectare plot (Table 1). This site appears to be exceptionally diverse. A mountain-wide survey of 1016 ha conducted in 1996 found an average of 6.3 fern species per hectare (range: 0-18) and recorded a total of 38 species, which represents the available regional pool for our study hectare (Bell and Bernhardt unpubl.). 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 (Palmer pers. comm.). More comparable levels of diversity were found in Massachusetts with 16-21 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 Nielson 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 10926), 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 m², calculated by r/R, as a measure of growth habit. 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). The values of r/R were found to correspond well with our observations in the field of the tendency of different species to form dense clumps.

Each species was characterised 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, rocky 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 from a high degree of environmental specificity combined with a clumped 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 of total area. The difference between the two curves represents the contribution of spatial structure or species aggregation to the form of the species-area curve, compared to the effect of sample size alone.

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 1-m 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). Randomisation of the species by sites matrix causes species to occur both randomly and independently whereas the variance test assumes only 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 correlationdistance relationship is a flat line without any distance decay. 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 neighbouring 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. *Athyrium filix-femina* (AFF) is positively associated with *Dryopteris carthusiana* (DCA), *Osmunda cinnamomea* (OCI) and *Polystichum acrostichoides* (PAC), while DCA also co-occurs with OCI, *Dryopteris intermedia* (DIN), and *Gymnocarpium dryopteris* (GDR). *Cystopteris bulbifera* (CBU) and *Adiantum pedatum* (APE) also tend to occur together, whereas *Dryopteris marginalis* (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 based on



Fig. 2. The spatial distributions of six species in the hectare. Orientation of the hectare is the same 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.

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

a centroid linkage method; it also expresses the consensus of six trees constructed using different clustering methods. APE-CBU-BVI (Botrychium virginianum), 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, since each species in a group still has its own 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 Figs 6A and B. 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 (DMA) 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 40 sites. However, they tended to fall within the cluster of points formed by the 10 common species, with the exception of Pteridium aquilinum (PAQ) 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 and would have a high positive association with DMA. Cystopteris fragilis (CFR) seems to belong with the APE-CBU-BVI-PAC group, while the remaining species are found with the group occupying the wetter, south-west portion of the site. Fig. 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 (unpubl.) 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_E^2). There was no relationship between these

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 Expected variance Variance of null model V _a /V _a	$0.40 \\ 0.42 \\ 0.42 \\ 0.95$	1.92 1.60 1.62 1.20	3.53 2.29 2.29 1.54	5.57 2.62 2.54 2.13	5.56 2.74 2.78 2.03	5.26 2.73 2.93 1.93	



Fig. 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.

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 five 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.

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Environmental structure

Soil conditions varied widely within the hectare: soil moisture ranged from 13 to 87% among the 400 samples (mean 48%); soil fertility by bioassay with *Chlamy-domonas* 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.

The patchy distribution of environmental conditions and of diversity is best appreciated from maps (Fig. 9). The strong topographic gradient which characterises 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 alkaline soil corresponding to a shallow valley which appears to be a temporary stream bed. More acidic soil



Fig. 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.



Fig. 6. The affinity of each species for particular soil conditions, 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. Open squares represent individual 5 m quadrats, displaying the range of conditions found in the entire hectare. A. fertility vs moisture. B. pH vs moisture.

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 to 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 characterised 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 primarily 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 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



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

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Fig. 8. Average variance of environmental conditions among pairs of 5 m quadrats as distance increases. A. soil pH, B. soil fertility, C. soil moisture.

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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 5 m 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 (Figs 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 second condition, occurrence of species in the sites to which they are best adapted, may be only partially met. The restricted spatial distributions of species which occur only in the wet corner or only on the slope provide indirect evidence that selection has acted to sort species according to environment (Fig. 2). The decrease of the specific correlation between sites with distance (Fig. 4) reflects this patchiness of species distributions. Moreover, a closer examination of the sites occupied by each species showed that fern species have different affinities for soil conditions (Fig. 6). To determine whether species tend to grow in sites where they are most competitive would require extremely complex competition experiments using a wide variety of environments.

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 any given site and blur the relationship 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. 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 >1 ha. Bell and Bernhardt (unpubl.) 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-fertilisation (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 (e.g. Osmunda, Matteucia) or very dense clumps made up of many stems, in which individual plants can scarcely be distinguished (e.g. 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

A. Fertility Moisture В. 12 12 1 100 100 - 12 22 22 23 25 12 12 100 100 100 医腺液 33 22 200 BB 200 100 100 12 **10 10 10 10 10 10 10 10 10 10 10** pH D. Diversity С. 頭鷹 199 BR 100 8 調願 10 10 調整部 篇 28 K 277 (C) 10 图 彩刻 篇 個 38 53 10 10 11.00 100 顧顧調調要 855 332 00

Fig. 9. The spatial structure of soil conditions and diversity among 5 m quadrats of the hectare. A. Soil fertility varies from 0 (white) to 659 (dark green); B. soil moisture varies from 13% (light blue) to 87% (dark blue); C. pH varies from 4.3 (red) to 8.2 (blue); D. the number of species varies from 0 (white) to 6 (dark purple). Orientation of the hectare is the same as in Fig. 1.

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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
5×5	*** rock (-)	* wood (+)	*** moisture (+)	
	*** wood (-) *** mud (+)	* mud (+)	*** fertility $(-)$	N.A.
10×10	*** rock (-)	* wood (+)	*** moisture (+)	* moisture $(-)$
	*** wood (-)		*** fertility $(-)$	* fertility (+)
	*** mud (+)			
15×15	* rock (-)	* water (+)	*** moisture (+)	* pH (-)
			*** fertility $(-)$	* moisture (-) * fertility (+)
20×20	_	_	*** moisture (+)	_
			*** fertility (-)	
25×25	_	_	*** moisture (+)	_
			*** fertility (-)	

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, emphasise 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 may be predominating 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 et al. 1988, Palmer 1990, Lechowicz and Bell 1991). If species are in fact restricted to very specific soil types but there is high soil heterogeneity within quadrats, then the environmental tolerance of each species will be overestimated using mean soil conditions (Palmer and Dixon 1990).

It is clear that environmental heterogeneity does affect species diversity in many situations. Rosenzweig (1995) reviews several studies which have found a relationship between species diversity and number of habitats, and argues that habitat diversity is the primary cause of most published species-area curves. However, in order to progress further in understanding and predicting the pattern, it will be important to better operationally define the systems under study and to compare different organisms and different scales. 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 (Palmer and White 1994a). Rosenzweig (1995) also argues that the causative relationship between species and habitat diversity may actually be the inverse of our intuitive expectation. Greater species diversity may cause us to observe greater habitat diversity. The more species there are, the more finely they will subdivide the available resources, such that researchers will observe more "apparent" habitat types. Physical and chemical environmental variables are continuous and may be infinitely subdivided by organisms. This idea provides a further argument for using repeatable, qualitative measures of environmental variation over a range of scales, rather than habitat classifications.

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 suggests that most fern species have an affinity for damp, shady places, as one would expect. Bell and Bernhardt (unpubl.) 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 fertilised fields (e.g. Tilman 1987), which is not the case here. 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 organisation 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.

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.

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