FERN COMMUNITY ASSEMBLY: THE ROLES OF CHANCE AND THE ENVIRONMENT AT LOCAL AND INTERMEDIATE SCALES

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Abstract. We evaluated the roles of the abiotic environment and dispersal in the assembly of fern communities at contrasting spatial scales within an old-growth, temperate deciduous forest. Specifically, we examined correlations among the geographic location of sampling plots separated by either 135–3515 m (mesoscale) or 4–134 m (fine scale), the abiotic environmental characteristics of the plots, and their constituent fern species. Ferns had predictable distributions along a soil moisture gradient at both spatial scales: six of eight common fern species showed repeatable environmental optima along the soil moisture gradient. By sampling in such a way as to decouple the correlation between distance and environmental variation, we showed the dominant role of environmental variables such as soil moisture in determining fern distributions at the mesoscale. At the fine scale, however, strong spatial autocorrelation in the abiotic environment precluded assigning any definitive role for either dispersal or environmental determinism alone in affecting fern distributions. The expectations of neutral theory that are rooted in dispersal limitation and those of niche theory that are rooted in environmental adaptation converge at fine spatial scales where natural environments have strong spatial structure. The structure of the environment at fine spatial scales may foster the persistence of dispersal-limited plants in the community; neighboring environments are likely to be similar, and thus suitable for propagules dispersing short distances. While patterns of fern distribution in this locality are not consistent with purely neutral or random models of species coexistence, alternative models that rely on strict niche requirements without accounting for dispersal effects and the inherent spatial structure of the environment are inadequate because they neglect the important interaction of these factors. This outcome supports the relevance of developing theory that considers the joint effects of environmental determinism and dispersal on the distribution and abundance of plant species.

Key words: dispersal limitation; ferns; fine scale; mesoscale; neutral theory; niche; partial ordinations; pteridophyte; spatial structure.

INTRODUCTION

The relative importance of the abiotic environment and dispersal in affecting the distributions of plant species is currently a topic of active debate (e.g., Bell 2001, Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004, Kneitel and Chase 2004). Traditional explanations of plant distributions, which assume that interspecific differences in niche requirements underlie patterns of species distributions, have emphasized the role of the abiotic environment (e.g., Whittaker 1967, Silvertown et al. 1999, McKane et al. 2002, Potts et al. 2004). More recently, spatially explicit models have stimulated a reconsideration of the possible, perhaps dominant, effects of dispersal on community assembly (Bell 2001, Hubbell 2001). Patterns of spatial aggregation similar to those expected in niche-assembled communities can occur in dispersal-

limited populations with approximately equal competitive abilities (Chave and Leigh 2002), or in populations having a competition vs. dispersal trade-off (Chave et al. 2002), with or without species-specific responses to the underlying environment (Levine and Rees 2002). Unfortunately, it can be quite difficult to identify the actual roles of stochastic and deterministic processes involved in determining plant distributions and community assembly, especially when the patterns generated from different processes are expected to be very similar (Chave et al. 2002, Gilbert and Lechowicz 2004).

Recent attempts to assess the relative importance of dispersal limitation and the abiotic environment in determining plant distributions fall into two broad categories. The simplest approach involves fitting curves to some particular causal model, and inferring that a single mechanism acts on species distributions. For example, neutral spatial models interpret species distributions to be caused solely by dispersal limitation, irrespective of any adaptive differences among species (Chave and Leigh 2002, Condit et al. 2002). In this case, spatial distances are used as a surrogate for dis-

persal through space over time, and the change in species distributions between sampling points is thus regressed against the distance between points to infer dispersal processes. A second approach involves evaluating multiple mechanisms by simultaneously examining the correlations among plant distributions, the underlying environment, and the spatial proximity of sampling points (Borcard et al. 1992, Duivenvoorden et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004), or by attributing distributions of juveniles to both the abiotic environment and proximity to parent plants (Arii and Lechowicz 2002).

These two approaches to modeling the basis of plant distributions lead to quite different interpretations. In the case of a neutral model, the fairly good fit of the model over large distances suggests that dispersal alone, without any environmental influence, largely determines plant distributions (Condit et al. 2002, Chave 2004). A priori restriction of sampling to particular habitat types (e.g., Harms et al. 2001, Condit et al. 2002) allegedly allows exploration of the role of dispersal within a spatially dispersed set of ''uniform environments.'' However, this method is prone to indicate false correlations if changes in environmental conditions occur predictably with distance between points (Gilbert and Lechowicz 2004), as has been shown in a number of studies (e.g., Bell and Lechowicz 1991, Bell et al. 1993). Similarly, an approach that correlates environmental gradients to species without accounting for spatial aggregation may ignore the important roles of spatial processes, such as local dispersal (Legendre and Legendre 1998). The presence of spatial structure, in both plant distributions and in the natural environment, thus raises uncertainty about the spatial scales at which any independent or joint effects of environmental gradients and dispersal are relevant to species distributions and community assembly.

Statistical models that set environmental determinism and dispersal hypotheses against each other, while allowing natural spatial variation in the sampled environment, have shown that the environment appears to be more important than dispersal at large spatial scales (Tuomisto et al. 2003). However, at scales >1 ha and less than tens of square kilometers (the mesoscale), the effects of the environment and dispersal are difficult to distinguish because of a common correlation between environmental gradients and the geographic distribution of sampling points (Duivenvoorden et al. 2002). Gilbert and Lechowicz (2004) used a spatially structured sampling design to break the correlation between the environment and the geographic location, and were able to show that environmental correlates of plant distributions remain important at the mesoscale, but spatial correlates do not. These studies of diverse plants (from trees to ferns to graminoids) in both temperate and tropical regions suggest that, at the mesoscale and the large scale, the abiotic environment can, in fact, be as important in affecting plant distributions

as any simple spatial effects arising from dispersal acting independently. This contrasts with the dominant role for stochastic factors associated with dispersal that is predicted at larger spatial scales in neutral models (Bell 2001, Hubbell 2001).

The conflicting evidence to date leaves open some significant questions, all connected to the possibility that the balance of stochastic and deterministic factors influencing plant distributions depends on spatial scale. First, how does the relative influence of the abiotic environment or dispersal on the assembly of plant communities change with the spatial scale sampled, especially at local spatial scales? Second, to what degree can the abiotic environment and dispersal limitation be separated as independent factors affecting community composition at different spatial scales?

In this study we investigated these questions about the importance of dispersal and environmental determinants of plant distributions. We extended our analysis of previously published sampling data on ferns in a forest understory, which were sampled at a mesoscale (distances of 135–3515 m), in plots in which the correlation between the geographic location and the abiotic environment was eliminated (Gilbert and Lechowicz 2004). To contrast these mesoscale data, we sampled ferns within a single hectare in the same forest, with sampling sites in this fine-scale survey separated by 4–134 m. These data allowed us to test the presence and consistency of environmental and spatial patterns within and between contrasting spatial scales. In addition, the fine-scale survey allowed us to determine if abiotic limits to plant distributions can complement dispersal limitation, by examining the spatial distribution of the environment at a spatial scale consistent with dispersal from parent plants over only one generation.

Ferns offer a number of advantages as a focal community in this study, and have been used in a number of previous studies that compare environmental and dispersal effects (e.g., Tuomisto et al. 2003, Gilbert and Lechowicz 2004). Many of the biotic factors (pests, pathogens, herbivores) that may be important in determining the distribution and abundance of other plant groups have little or no influence on ferns (Lellinger 1985, Barrington 1993), which simplifies the assessment of environmental influence. The distribution and abundance of ferns have traditionally been attributed to the abiotic environment, with climatic differences acting at continental and regional scales (Dzwonko and Kornas 1994, Marquez et al. 1997), and edaphic conditions cited at local scales (Wherry 1920, Petersen 1985, Odland et al. 1990, Tuomisto and Poulsen 1996, 2000, Greer et al. 1997, Ruokolainen et al. 1997, Richard et al. 1999). In terms of local distribution and abundance, any role of dispersal limitation has generally been discounted because of the high vagility of airborne fern spores (Zobel et al. 2000). However, Tuomisto et al. (2003) have recently shown strong spatial
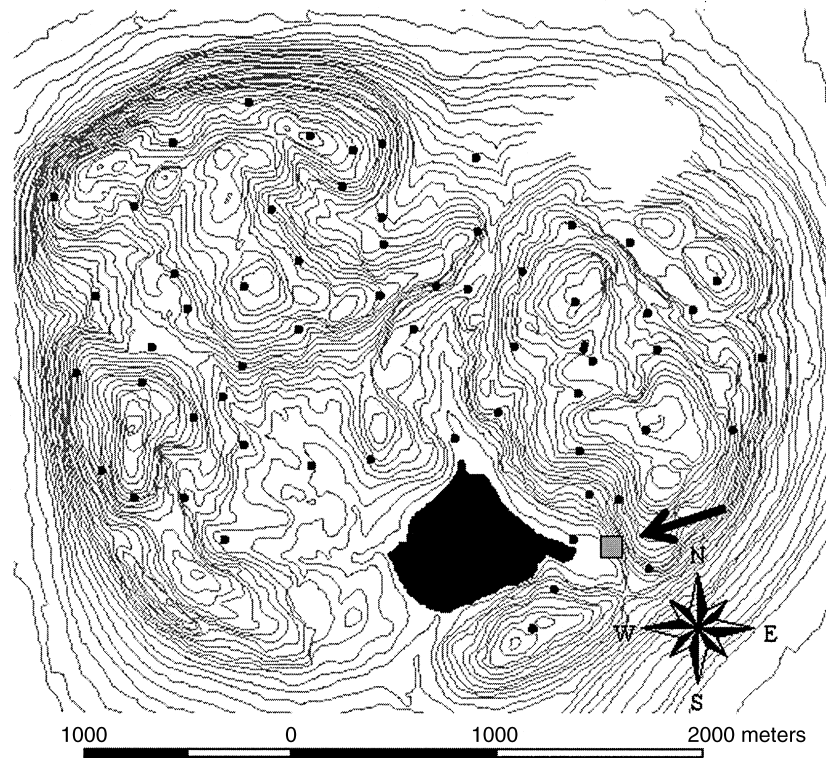
FIG. 1. Spatial distribution of 57 sampling locations (represented by dots) that contained fern species in the mesoscale survey of the Gault Nature Reserve, Québec, Canada. The arrow indicates the position of Botany Bay, the hectare in which the fine-scale survey was situated. Contours are at 10-m intervals.

turnover in ferns at local scales that could not be attributed to environmental differences. Ferns thus provide a good opportunity to investigate the relative influence of dispersal and the abiotic environment in determining species distribution and abundance across different spatial scales.

Three aspects set this work apart from previously published research (e.g., Gilbert and Lechowicz 2004, Tuomisto et al. 2003). First, Gilbert and Lechowicz (2004) broadly described the mechanisms influencing the mesoscale distribution of six different plant groups, only one of them being seedless vascular plants. Here we focus on the underlying determinants of variation specifically in fern communities, drawing upon details of the autecology and biology of ferns to assess factors underlying species distribution and abundance. Second, comparing surveys at two distinct scales allows us to directly assess the scale dependence of patterns and underlying mechanisms structuring fern communities. Sampling fern communities at both the mesoscale and fine scale not only enables weighting of competing mechanisms (dispersal vs. environmental determinism), but also surveys a range of environmental conditions at varying scales, and thus is more representative of the ecological conditions of the species considered. Finally, the methodological approach used in the present study is novel in itself and yields new in-

sights. Only by surveying at these contrasting spatial scales can we identify the independent and interactive effects of the abiotic environment and dispersal on a community assembly. In other words, our multiscale sampling approach allows us to evaluate the independent effects of environmental determinism and dispersal when they do not confound each other, and also to determine the degree to which these two processes may work in conjunction in a locality.

METHODS

Study sites

We worked at the Gault Nature Reserve (GNR; McGill University), an area of rugged topography, 10 km² in extent, located on Mont Saint Hilaire (MSH; 45°32′ N, 73°08′ W) near Montréal, Québec, Canada (see Plate 1). The geology, microclimate, hydrology, vegetation, and natural history of the reserve have been described elsewhere (Maycock 1961, Rouse and Wilson 1969, Feininger and Goodacre 1995, Arii et al. 2005). Of the 60 fern species present in Québec (Fleurbec 1993), 38 are found at GNR (M. J. Lechowicz, M. J. Waterway, and G. Bell, *unpublished data*).

For this study we sampled the GNR in two distinct ways. First, in the summer of 2000, we conducted a fine-scale survey of one species-rich hectare that con-

PLATE 1. Botany Bay on Lac Hertel in Gault Nature Reserve, Mont Saint Hilaire, Québec, Canada. The hectare in which the fine-scale study of the fern community was done lies part way up the slope at the left center of the image. Photo credit: Francis Lépine.

tained 20 fern species (Fig. 1). This hectare consisted of wet, flat terrain in the southwest corner rising to a steep, rocky slope in the opposite corner. The site was divided into a grid of 100 10 × 10 m plots surveyed in projected map view, but since the topography is rugged, the effective dimensions of the plots on the ground ranged up to 12 m on a side. We considered only a subset of consistent 8 × 8 m plots as surveyed on the ground, each with its origin at the northwest corner of a 10 × 10 m plot in map view. This yielded an array of 100 8 × 8 m plots, not quite contiguous, within the hectare. These 8 × 8 m plots were further subdivided to a smaller grain of 4 × 4 m quarters, of which there were a total of 400 in the hectare. The grain, extent, and arrangement of the plots allowed us to test for spatial structure of the abiotic environment and fern distributions at a fine scale.

Our second survey, in the summer of 2002, was set at the mesoscale and designed to decouple the correlation between geographic distance and environmental change observed in many similar studies. We used a digital elevation model of the reserve in concert with geographic information system (GIS) software to identify potential sample sites (50-m^2 circular plots), in broadly defined environmental classes based on terrain attributes (aspect, slope steepness, and slope position; cf. Grigal et al. 1999). We took these physiographic variables as indicators of a more comprehensive set of environmental variables, which were to be sampled later. In deciding potential sampling sites, we excluded all water bodies and any sites situated within 10 m of

trails, the shore of Lac Hertel inside the reserve, or the outer perimeter of the reserve. We selected sites so that any correlation between site characteristics representing the abiotic environment and distance would be avoided in the data set. For example, we chose a south-facing, steep, midslope site to have both environmentally similar and dissimilar sites evenly distributed across near to far distances. We also chose sites that ensured the entire reserve was well represented. We iteratively tested tentative sampling designs using Mantel tests until there was no detectable correlation between distance and site characteristics. We assessed the selected sites in the field in the spring of 2002, and used initial on-site estimates of slope, aspect, soil moisture, and humus richness to again test the success of our sampling design. Gilbert and Lechowicz (2004) provide additional details on this survey.

Geographic distances between sampling points in the mesoscale survey ranged from 0.135 to 3.515 km (Fig. 1), with the lower limit determined by the minimum distance at which we could ensure a decoupling of site characteristics and geographic distance. The sampling design reduced the correlation between environmental difference and geographic distance to trivial levels; once a Bonferroni correction was applied for multiple comparisons, only nitrate showed a significant, but minor, correlation with distance (Mantel $r = 0.14$). Full details on the decoupling method are presented in Gilbert and Lechowicz (2004). We did not place sample points from the mesoscale survey on the 1-ha survey;

the two data sets were gathered in the same tract of forest but do not contain redundant information.

Data collection

In the fine-scale survey, the percent cover of fern species was determined from visual estimates by one of three observers, with 15% of plots (60 quarters) reassessed for consistency by all three observers. Three soil samples were collected at random locations in each 4×4 m quarter by removing leaf litter and taking ~500 mL of soil from the top 8 cm of the soil profile. These samples were pooled to form one soil sample per quarter, for a total of 400 samples for the entire hectare. We stored the soil samples in plastic bags and refrigerated them at 4°C until ion analyses. Soil pH was measured with a Fisher silver chloride pH probe (Fisher Scientific International, Nepean, Ontario, Canada) and nitrate with a Thermo Orion nitrate electrode, model 93-07, combined with a Thermo Orion Ag/AgCl double-junction reference electrode, model 90-02 (Thermo Orion, Beverly, Massachusetts, USA), all connected to a Fisher AR 25 Ion meter. Thermo Orion ionic strength adjuster (2 mL) (Orion catalogue number 13-641-850) was mixed into each sample. We also measured soil moisture in three random locations within each 16-m² quarter, using a Delta-T Devices type ML2x theta probe (Delta-T Devices, Cambridge, UK) twice in the season, once in early August, and again in mid-September (Karst 2001). We used these six measurements to calculate the mean and coefficient of variation of soil moisture.

In addition to the surveyed measurements, we also described the canopy conditions in each 16-m² quarter based on a previous georeferenced survey of every tree in the hectare (Duguay et al. 2001). To calculate interpolated values of canopy conditions for each quarter, we used the "inverse distance weighted interpolation" in the spatial analyst extension of ArcView 3.2 (ESRI, Redlands, California, USA). We calculated (1) the diameter at breast height (dbh) for each of the four most common tree species (*Acer saccharum*, *Fagus grandifolia*, *Quercus rubra*, and *Tsuga canadensis*); and (2) the degree of damage to the tree canopy caused by the 1998 ice storm, on a five-point scale (5 = most damage), for trees >10 cm dbh (cf. Duguay et al. 2001). To summarize, environmental variables for each 16-m² quarter of the fine-scale survey included the mean and coefficient of variation of soil moisture, soil nitrate, soil pH, percent cover of rock and coarse woody debris, median soil depth, basal area of the four dominant tree species, and estimated canopy damage.

In the mesoscale study, 69 50-m² circular plots were placed at each sampling point, of which a total of 57 plots contained fern species. The percent cover of species was determined with visual estimates, using the average cover estimated by two independent observers, with a subset of plots reassessed for consistency by a third observer. In total, there were 11 environmental variables, measured as follows. We calculated the mean soil moisture from three soil moisture measurements taken at each sampling point to a depth of 5 cm in early September 2002, using an ML2x theta probe (Delta-T Devices, Cambridge, UK). We pooled four soil samples, taken to a depth of 8 cm, from each site and analyzed loss on ignition at 500°C (as an estimate of soil organic matter), pH, NO_3^-, NH_4^+, P, K, Ca, and Mg. At each site we also measured slope and light regime, using hemispherical photos from the plot center as an indicator of light availability. All methods are detailed in Gilbert and Lechowicz (2004).

Statistical analysis

We used three separate analyses to examine the relationship between geographic location (used to infer dispersal limitation [Borcard et al. 1992, Tuomisto et al. 2003, Gilbert and Lechowicz 2004]), environmental gradients, and fern species distributions at the two scales. First, on both data sets, we used partial canonical correspondence analyses (CCA) to distinguish between species distributions that can be modeled with a spatial trend-surface analysis and those that can be modeled along environmental gradients (Borcard et al. 1992). This approach uses a CCA to determine the variation in fern distributions that is explained by environmental gradients alone (i.e., with the variation attributable to a spatial model removed), and conversely, the variation that is explained by a spatial model alone. Spatial patterns arising from dispersal limitation are inferred by the spatial model used in this analysis. The remaining variation can either be explained by both variables (i.e., spatially structured environmental gradients), or is unexplained variation. Overall, the partial CCA models four distinct components of variation in plant community composition: (1) space only, attributed to dispersal patterns; (2) environment only, attributed to environmental determinism; (3) space correlated to environment; and (4) unexplained variation. Unexplained variation may be produced by unmeasured environmental variables (Legendre and Legendre 1998), as an artifact of the CCA (Okland 1999), or due to a model lack of fit.

The spatial model of the partial CCA is a cubic regression that is commonly applied in trend-surface analysis (Legendre and Legendre 1998). In this approach, site coordinates are first centered by subtracting the geographic centroid of all site coordinates, so that the center of the sampling map is assigned coordinates $X = 0$, $Y = 0$. The centered Universal Transverse Mercators (UTM) of the sites are then used as predictor variables in a cubic regression model (i.e., $\hat{y} = b_1 X + b_2 Y + b_3 X^2 + b_4 XY + b_5 Y^2 \ldots + b_8 X^3 + b_9 Y^3$). For the environmental portion of the partial CCA, we used those gradients and factors measured in each survey, with variables log transformed when necessary. Within the CCA, this approach will model unimodal or linear trends of species abundance along these spatial and

TABLE 1. Average percent cover of fern species surveyed at mesoscale and fine scale within the Gault Nature Reserve, Québec, Canada.

Species	Abbreviation	Mesoscale	Fine scale
Adiantum pedatum	APE	0.39	5.12
Athyrium filix-femina	AFF	0.36	2.26
Botrychium matricariaefolium	...	<0.01	0
Botrychium virginianum	BVI	0.02	0.02
Cystopteris bulbifera	CBU	0.43	2.05
Cystopteris fragilis	CFR	0.05	0.03
Dennstaedtia punctilobula	DPU	0.09	0.01
Deparia acrostichoides	DAC	1.24	0.27
Dryopteris carthusiana	DCA	0.25	0.10
Dryopteris clintoniana	...	0.04	0
Dryopteris goldiana	DGO	0.16	0.03
Dryopteris intermedia	DIN	1.42	0.07
Dryopteris marginalis	DMA	0.75	1.37
Gymnocarpium dryopteris	GDR	0.03	0.15
Matteuccia struthiopteris	MST	1.31	0.04
Onoclea sensibilis	OSE	0.91	0.12
Osmunda cinnamomea	OCI	1.07	0.37
Osmunda claytonia	...	<0.01	0
Osmunda regalis	...	0.29	0
Phegopteris connectilis	PCO	0.12	0.01
Polypodium appalachianum	...	0.01	0
Polypodium virginianum	...	0	<0.01
Polystichum acrostichoides	PAC	0.28	0.23
Pteridium aquilinum	PAQ	0.18	0.01
Thelypteris palustris	...	0	0.04
Woodsia elvensis	...	0.01	0

Notes: The mesoscale and fine-scale surveys comprised 69 50-m^2 plots distributed over 10 km^2, and 400 16-m^2 plots distributed over 1 ha, respectively. Species nomenclature follows the Flora of North America Editorial Committee (1993). Abbreviations are given for ferns occurring in both surveys.

environmental variables. All environmental and spatial variables were subject to forward selection in the partial CCA for each survey, with both surveys having nine spatial variables and the fine-scale and mesoscale surveys having 12 and 11 environmental variables, respectively. Only sampling sites with ferns present were used in CCAs, as required for this type of analysis.

In our second analysis we assessed the spatial autocorrelation of the abiotic environment in our fine-scale survey. To do this, we used a Mantel test to model a trend between geographic distance and environmental change. Environmental change was calculated as the Euclidean distance of all the standardized environmental variables that were significant in the fine-scale CCA (McCune and Mefford 1995). Geographic distance was calculated as the Euclidean distance between sites to produce the shortest on-the-ground distance between the centers of each pair of plots. A similar Mantel test of the mesoscale survey was unnecessary because of the sampling design. It is important to note that the Mantel test is not meant to compare directly to the ordination results, as it measures a different variance and reports weaker correlations than tests on raw data (Dutilleul et al. 2000). We use it instead to look at the nature of the clustering of similar environments over geographic distance and to complement the results of the ordination.

Our third analysis was aimed at determining the consistency of the environmental optima of fern species.

Soil moisture was the single strongest predictor of fern distributions at both scales (see *Results*). We ran a CCA for each of the two data sets, with soil moisture as the only explanatory variable, and included only species occurring at least three times in both data sets (13 species in total). Using the calculated values for species positions along the first CCA axis (necessarily representing soil moisture), we examined the consistency in species optima along the soil moisture gradient by testing the correlation between the fine-scale and mesoscale data set, with each species acting as one observation. We illustrated these results graphically by plotting the distribution of the most common fern species (occurring at least eight times in each survey) along the soil moisture gradient.

RESULTS

The total aerial coverage of all the fern species in the fine-scale survey was ~11%, compared to 9% in the mesoscale survey. Abundances of the individual fern species varied between the two surveys (Table 1). Voucher specimens can be found in the McGill University herbarium. Fern species richness ranged from 0 to 6 species per 16-m^2 quarter (86% of the 400 quarters had at least one fern species present) and from 0 to 7 species per 50-m^2 plot (83% of 69 plots had at least one fern species present) in the fine-scale and mesoscale surveys, respectively. In total, we found 20 species in the fine-scale survey and 25 in the mesoscale

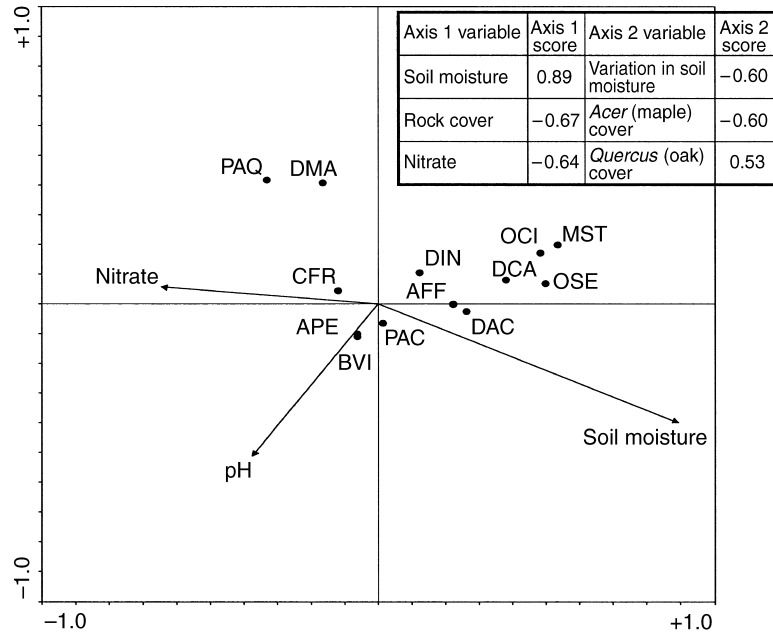| Axis 1 variable	Axis 1 score	Axis 2 variable	Axis 2 score
Soil moisture	0.89	Variation in soil moisture	−0.60
Rock cover	−0.67	*Acer* (maple) cover	−0.60
Nitrate	−0.64	*Quercus* (oak) cover	0.53

FIG. 2. Canonical correspondence analysis (CCA) biplot and associated environmental biplot scores of fern species surveyed at a fine scale within the Gault Nature Reserve, Québec, Canada. Note that only those environmental measurements common to both the fine-scale and mesoscale surveys are represented with vectors, and biplot scores are given for the three most dominant environmental variables on each axis. See Table 1 for species abbreviations.

survey. Fern richness showed moderate correlations to soil moisture in the fine-scale and mesoscale surveys ($r = 0.435$, 0.481, respectively; both $P < 0.001$).

At the fine scale, all the available environmental variables were significant ($P < 0.001$) and explained 26% of the variance in the fern species distributional data. The first axis of the CCA was most strongly correlated to mean soil moisture, and secondarily to soil nitrate concentration (Fig. 2). The spatial model, represented by all the spatial variables, was also significant and explained 30% of the variation in species distribution ($P < 0.001$). An obvious spatial trend existed in soil moisture and nitrate (environmental data including spatial effects: axis 1 biplot scores of the two variables were 0.89 and −0.64, respectively; environmental data constrained by the spatial model were 0.004 and 0.002, respectively). The explanatory power of soil moisture alone decreased by 90% when its covariance with the spatial component was removed, reflecting the strong topographic influence on soil moisture within the site. The wet-to-dry gradient extended from the dry and rocky slope of the northeast corner of the hectare to the moisture-saturated, lower southwest corner. Soil nitrate concentrations were generally lowest in the wet parts of the hectare, with pockets of high concentration situated in the upper part, but were patchier than that of soil moisture. Axis 2 of the environmental CCA was most strongly correlated to the within-plot variability in soil moisture, and secondarily to *Acer saccharum* cover (Fig. 2).

Similarly at the mesoscale, an environmental model (with the variables pH, NO_3^-, P, K, slope, soil moisture, and loss on ignition of soil retained in the forward selection process) was significant, and explained a total of 42% of fern distribution ($P < 0.001$). The spatial model was also globally significant and explained 20% of fern distributions at the mesoscale (spatial variables x, x^2, y^2x, and y^2 retained, based on forward selection). Slope steepness, which was highly negatively correlated to soil moisture, was most strongly correlated with CCA axis 1, followed by soil moisture (biplot scores of 0.95 and −0.86 respectively; Fig. 3). Soil pH and nitrate were negatively correlated with CCA axis 2. At both survey scales, fern species distributions were strongly affected by the soil moisture gradient.

The proportions of the four distinct components explaining fern distributions varied between the two scales (Fig. 4). At the mesoscale, the "environment correlated with space" explained the least amount of variation, just less than 7%, but this was a necessary outcome of our sampling design. The remaining explained variation was attributed mainly to the abiotic environment (34%). In contrast, at the fine scale, the environment correlated with space explained the largest portion of variation of fern distributions (18%), followed by "pure space" (12%) and "pure environment" (7%). The amount of floristic variation explained by the environment, including the spatially structured environment, between the two scales differed by 16%. This could be due to a number of significant soil var-

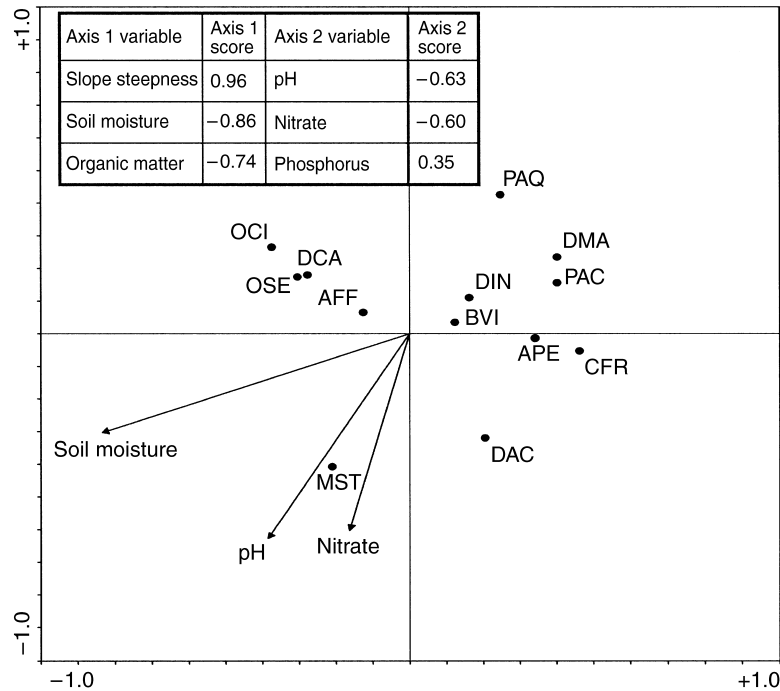| Axis 1 variable	Axis 1 score	Axis 2 variable	Axis 2 score
Slope steepness	0.96	pH	−0.63
Soil moisture	−0.86	Nitrate	−0.60
Organic matter	−0.74	Phosphorus	0.35

Fig. 3. Canonical correspondence analysis (CCA) biplot and associated environmental biplot scores of fern species surveyed at a mesoscale within the Gault Nature Reserve, Québec, Canada. Note that only those environmental measurements common to both the fine-scale and mesoscale surveys are represented with vectors, and biplot scores are given for the three most dominant environmental variables on each axis. See Table 1 for species abbreviations.

iables (i.e., pH, P, K, slope, and percentage lost on ignition) that were measured at the mesoscale but not at the fine scale. The correlation between the environment and geographic distance was also demonstrated by the Mantel test, which showed a significant change in environmental conditions with geographic distance ($r = 0.501$, $P < 0.001$). This is represented graphically in Fig. 5, illustrating that the median change in soil moisture for sites 4 m apart was <10%, but at greater distances, such as 100 m, there was >30% change in soil moisture. This variable dominated the first axis of the CCA for both the fine scale and mesoscale, with the first axes explaining 14% and 18% of fern distributions, respectively.

The positions of fern species shared by both surveys along a soil moisture gradient was strongly correlated ($r = 0.91$, $P < 0.001$; Fig. 6), indicating that species optima along the soil moisture gradient were highly

conserved between the two survey scales. A graphical view of distributions along the moisture gradient indicated that six of the eight common fern species shared by both data sets showed consistent environmental optima (Fig. 7). Segregation along this gradient was apparent among these species: *Cystopteris fragilis*, *Dryopteris marginalis*, and *Adiantum pedatum* occupied sites with lower soil moisture; *Polystichum acrostichoides* and *Athyrium filix-femina* were found mostly in sites with midranges of soil moisture; and *Onoclea sensibilis* was found at the wettest sites. The two species that did not show consistent soil moisture tolerances, *Deparia acrostichoides* and *Dryopteris intermedia*, did not respond to variation in soil moisture in either of the surveys.

DISCUSSION

At first glance it appears that the results from our fine-scale and mesoscale surveys differ in the relative
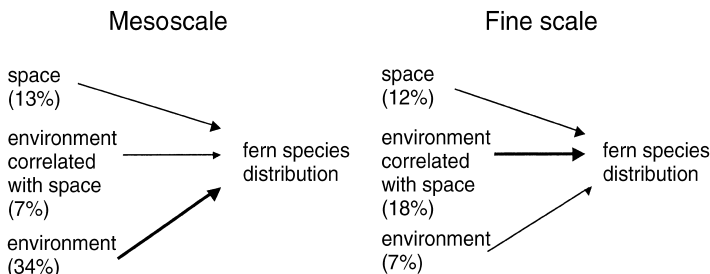
Fig. 4. Partitioning of explanatory components of variation in fern species distribution within the Gault Nature Reserve, Québec, Canada, based on partial canonical correspondence analysis (CCA) results. Note that some environmental variables differed between surveys. Variables used in the environmental and spatial (dispersal) components are given in *Methods*.
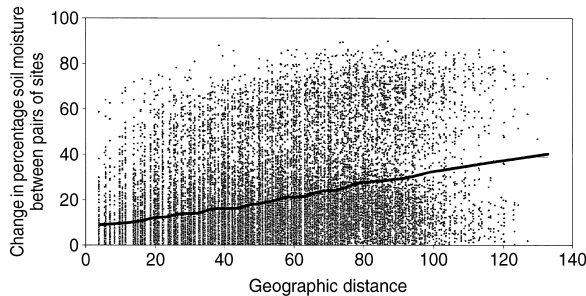
FIG. 5. Spatial structure of fine-scale variation of soil moisture within Botany Bay, the hectare in which the fine-scale survey was performed. The percentage change in soil moisture between pairs of sites was calculated as the Euclidean distance in soil moisture between two sites, or the absolute value of the difference in soil moisture. The displayed curve is a running median with a 0.1 sampling proportion.

importance of the effects of environmental determinism and dispersal on fern distributions (Fig. 4). However, for a number of reasons, we believe that there is, in fact, a scale-independent role of the abiotic environment in determining fern species distributions.

First, the fern species common to both of our surveys have similar relative positions along the soil moisture gradient regardless of sampling scale, as indicated by the strong correlation of species ordination scores and illustrated by species distributions along the ordination axes. This high correlation of soil moisture optima for fern species between the two scales is extremely unlikely by chance alone (with a probability of <0.001), indicating a consistent role for environmental determinism of fern distributions across spatial scales. This locally important role of soil moisture is also consistent with previous studies of ferns. For example, Greer et al. (1997) reported a separation among fern species along a soil moisture gradient in southeastern Ohio. Similarly, differences in the fern community were attributed to variation in soil drainage of 100-m^2 and 25-m^2 plots in Amazonian rain forests (Tuomisto and Poulsen 2000). At larger scales, Marquez et al. (1997) reported that water availability was an important factor underlying fern distributions on the Iberian Peninsula, Spain, and a humidity gradient was the main factor influencing differentiation of fern species in Rwanda (Dzwonko and Kornaś 1994). Given the moisture demands of gametophytes to complete fertilization (Page 2002) and the simple tracheary elements present in most ferns (Sharma 1988), it is not surprising that fern distribution is strongly linked to water regime. How then can we reconcile the apparent importance of soil moisture in determining fern distributions with the relatively low influence of the "pure environment" effect at the fine scale, compared to the mesoscale, in our locality?

The majority of the explained variation in our fine-scale survey is attributed to the covariance between distance and environment—in other words, to spatial

structure in the environment. Taken alone, this fine-scale survey could be interpreted as providing support for models positing either dispersal or environmental determinism as controls on community assembly. Because the covariance between distance and environment cannot be broken at the fine scale, it is impossible to know the independent effects of either factor. Specifically, in the range of 4–140 m at our site, it is impossible to separate the effects of dispersal from those of soil moisture, thus undercutting any "pure environment" signal of this important environmental variable. Nonetheless, the combined results from surveys at both spatial scales clearly indicate that these ferns do consistently segregate along soil moisture gradients. If stochastic dispersal processes alone were determining fern distribution, we would not expect any particular environmental gradient to structure fern communities at multiple scales, least of all a single environmental gradient.

Although we can identify a scale-independent role for soil moisture in determining fern distributions, our ability to separate the effects of dispersal and environmental gradients in general does appear to be scale dependent. Our results indicate that a purposefully designed sampling strategy can be effective in distinguishing the two effects at the mesoscale, but not at the fine scale. At the fine scale, the spatial structuring of the environment is too strong and cannot be eliminated among samples that are necessarily closely spaced. This association between environmental factors and topographic variation within the fine-scale survey area accounted for the high correlation between dispersal and environmental patterns in the partial CCA (Figs. 4 and 5). This result is troubling for the interpretation of fine-scale studies of controls on plant distribution. Environmental factors must be independent
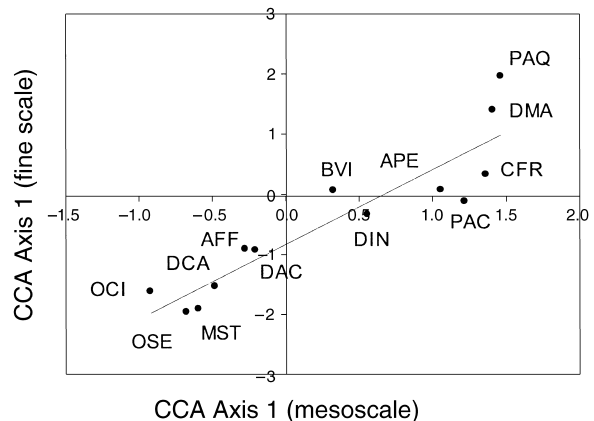

FIG. 6. Correlation ($r = 0.91$, $P < 0.001$) between fern species surveyed at both a fine scale and a mesoscale along a soil moisture gradient within the Gault Nature Reserve, Québec, Canada. Placements of individual species along the gradient were calculated from scores produced by a canonical correspondence analysis (CCA) of species constrained solely by soil moisture. See Table 1 for species abbreviations.
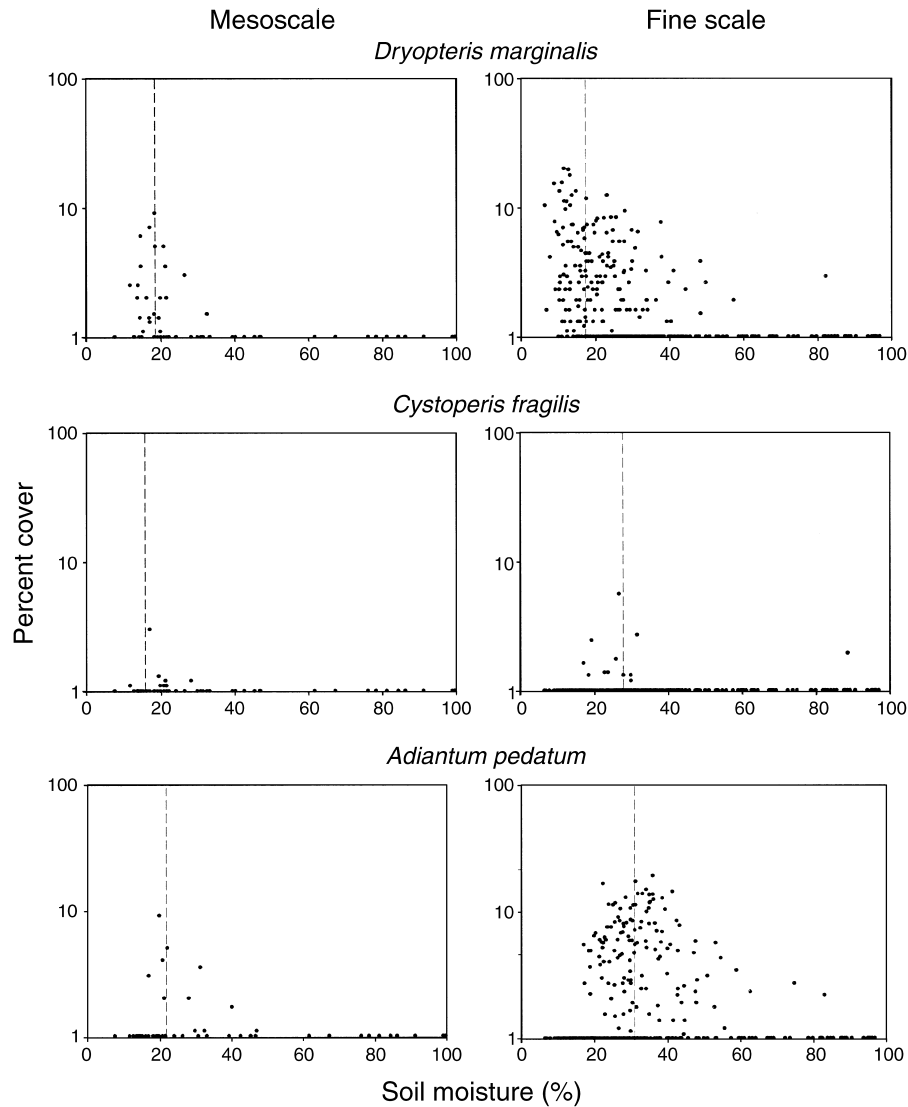
FIG. 7. Comparison of the percent cover of individual fern species along a soil moisture gradient. Graphs in the left and right columns represent fern species sampled at the mesoscale and fine scale, respectively, within the Gault Nature Reserve, Québec, Canada. Note that percent-cover values (*y*-axis) have been increased by 1 for visual representation on a log scale. The dashed line represents the mean value of soil moisture in plots in which the species occurred, weighted by its abundance.

of location if we are to unambiguously assess their role in determining plant distributions using available statistical techniques (Fortin et al. 1989, Legendre and Legendre 1998, Gilbert and Lechowicz 2004). Spatial autocorrelation, however, is an inherent property of the environment (Bell 1992) and is apparent at many scales (Bell et al. 1993), thus making it difficult to disentangle the correlates to plant distributions in nature. Indeed, from a plant's perspective, separating patterns based on environmental gradients and spatial autocorrelation at the fine scale may not properly reflect conditions that act on an individual plant and its offspring. This is the scale of plant neighborhoods where species interact through dispersal of pollen and seed, through clonal growth, and through competition, critical processes that

influence both the distributional ecology and evolutionary adaptation of plant populations.

The correlation between patterns predicted for dispersal limitation and environmental determinism at the fine scale may, in fact, work in favor of the dispersal-limited species central to neutral models of community assembly, but not necessarily in a neutral fashion. Species that are dispersal limited would likely benefit if their propagules encounter favorable environmental conditions close to the parent plant, as predicted by positive spatial autocorrelation of the environment. For example, two of the most abundant ferns in our survey hectare, *Adiantum pedatum* and *Cystopteris bulbifera*, spread by clonal propagation. The pattern of clonal distribution and the spatial structure of variation in soil
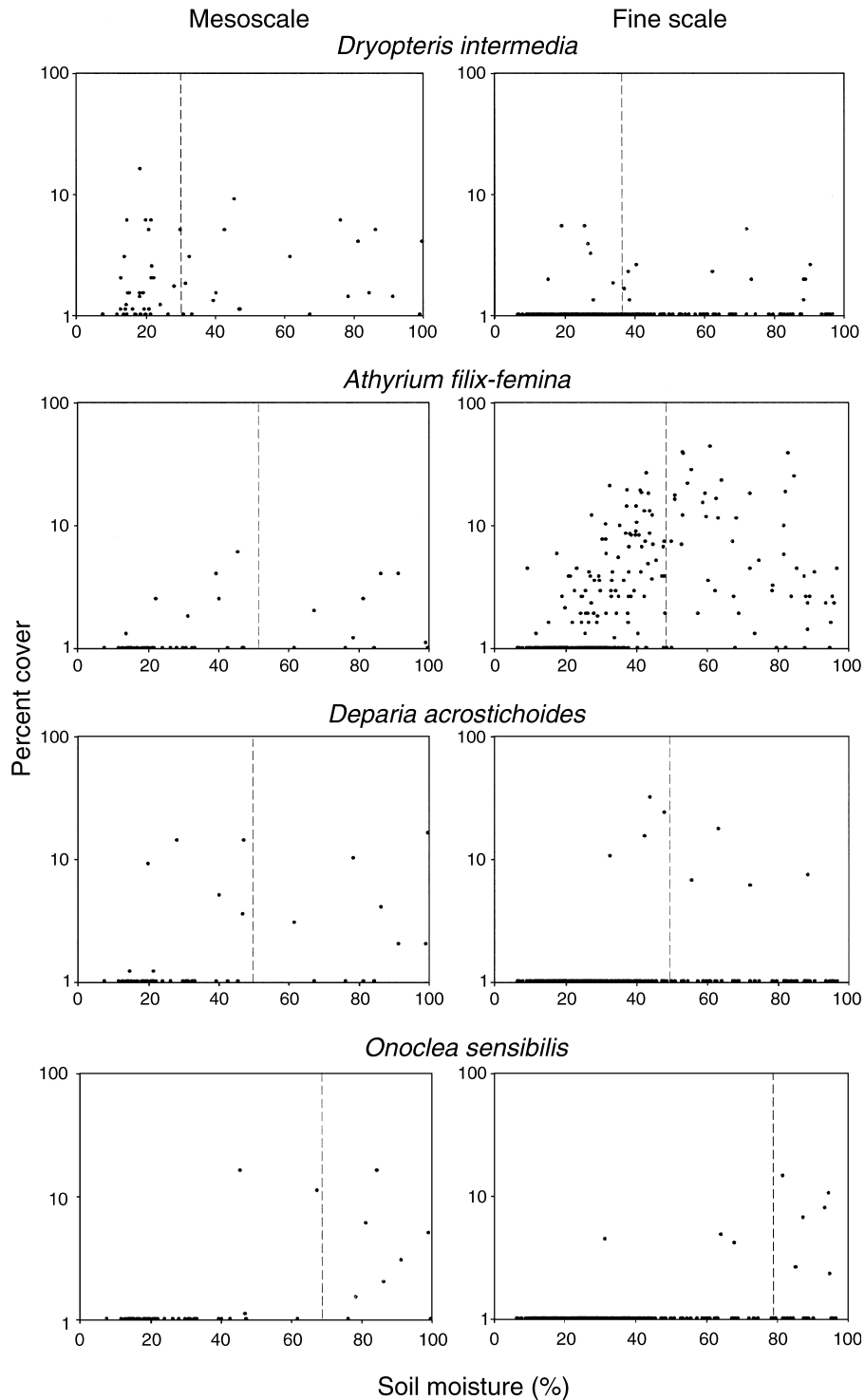
Mesoscale Fine scale

Dryopteris intermedia

Athyrium filix-femina

Deparia acrostichoides

Onoclea sensibilis

Percent cover

Soil moisture (%)

FIG. 7. Continued

moisture increase the likelihood of these ferns estab-lishing in favorable environments. At a fine scale, co-existence among ferns may be jointly determined by dispersal and environmental factors because the two factors are inextricably coincident at this scale. Indeed,

the close spacing of similar environments, coupled with the large change in environmental conditions from one corner of our study hectare to the other (a soil moisture range of 7 to 97%) may be responsible for the unusually high level of fern diversity in this particular hectare.

While long-distance dispersal offers advantages to species, such as avoidance of conspecific competition and other density-dependent effects (e.g., Janzen 1970, Harms et al. 2000), the advantage to short-distance dispersal in conjunction with environmental structure deserves further study. Given the strong dispersal limitation shown by a number of understory forest species (e.g., Vellend et al. 2003) and their consistent environmental affiliations, it appears that a research program organized simply to test neutral vs. niche theory may be fruitless in the end. Any sampling design for separating the independent effects of dispersal and the abiotic environment may be biased against understanding the more biologically relevant covariance of these factors in nature and how they complement one another in structuring understory plant communities.

Recently there has been an active debate over the roles of environmental determinism and neutrality in structuring communities (Bell 2001, Hubbell 2001, Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz 2004). Initially, neutral theory challenged the hypothesis that plants within an area show environmental adaptations, as spatial patterns used to infer niche relationships could be generated from a random walk (Bell 2001, Hubbell 2001). The consistent response of ferns to soil moisture and the importance of this gradient in both surveys indicate that, in this instance, a strict neutral model is incorrect at both scales (Fig. 6). In the face of evidence for strong environmental influences on species distributions (e.g., Terborgh et al. 1996, Tuomisto et al. 2003, Gilbert and Lechowicz 2004), Chave (2004) made the post hoc hypothesis that species adaptations to environmental gradients are not inconsistent with a neutral model so long as species act neutrally within a reasonably uniform environment. In our study, a uniform environment could not be defined even within an area of one hectare. Natural environments have a predictable, if sometimes noisy, pattern of change with distance; the farther apart are two points, the greater is the likelihood that their environments differ (Fig. 5). Likewise, fern species show a variety of ranges in soil moisture tolerance (Fig. 7), suggesting that different species have different ranges of environments that they would consider functionally "uniform" within their limits of tolerance. The division of the environment into "neutral" habitat patches does not appear to be possible from the perspective of the plants nor in terms of the underlying structure of natural environments.

In contrast to a neutral model, niche-based models propose that species occupy distinct environmental hypervolumes in which they are competitively superior (Hutchinson 1957). In the case of the ferns studied, we do see distinct, repeatable patterns of presence and abundance along environmental gradients (Figs. 6 and 7). However, it is important to note three apparent inconsistencies with any simple, deterministic niche model. The first is that the two surveys do show small differences in the range and modes of species' soil moisture tolerances, which does not support a strict niche model. This variation may be due to stochastic effects, including variation in both the environment and within species, and also to sampling error in each of the surveys (Clark et al. 2003). Second, both surveys showed significant dispersal effects, independent of the environment. Finally, there are a number of sites that do not contain a given fern species, even though the site appears to be within the appropriate soil moisture range. These "empty sites" may be due to a number of causes: multiple limiting factors, competition by other plant species, and stochastic processes, including those associated with dispersal. The level of unexplained variation in both surveys, consistent with previous studies (see examples in Borcard et al. 1992), also highlights the potential importance of other structuring mechanisms like density dependence and disturbance history. The relatively high explanatory power of CCA axes that were not dominated by soil moisture (12% and 23% for the fine-scale and mesoscale surveys, respectively) supports the proposal of multiple limiting environmental gradients. In particular, the stronger association of ferns to the soil variables measured in the mesoscale study suggests that edaphic factors are important in determining the niche space of ferns.

Our results convey two general messages about using sampling to distinguish the influence of environmental determinism and dispersal on plant distribution and abundance. First, by sampling at multiple scales, the relative importance of environmental and spatial processes working independently and in conjunction to affect plant distributions can be quantified. In particular, our fine-scale survey allowed us to quantify the joint importance and possible interaction of dispersal processes and environmental determinism, and our mesoscale sample allowed us to quantify their independent effects. Both of these results are essential in evaluating competing models of coexistence. Second, we have shown that fern species distributions in this locality are inconsistent with random and neutral models of species coexistence, but that at the same time, adopting a simple niche hypothesis without accounting for the effects of dispersal may also be problematic, due to the inherent spatial structure of the environment and the variability encountered in nature. More complex niche models, which incorporate the interactive effects of dispersal, competitive effects, and stochasticity (e.g., Levine and Rees 2002, Marquet et al. 2003, Etienne and Olff 2004, Kneitel and Chase 2004, Tilman 2004), offer a greater potential to explain our results. This eclectic perspective on the possible joint influence of dispersal and environmental determinism at different spatial scales may help reorient the ongoing debate over the roles of environmental niches and neutrality in community assembly (Bell 2001, Hubbell 2001, Condit et al. 2002, Tuomisto et al. 2003, Gilbert and Lechowicz

2004). Rather than testing "neutral vs. niche" models, we suggest that further research investigate the interaction between dispersal and environmental determinism affecting plant distribution and abundance.

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