The distance decay of similarity in biogeography and ecology

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Abstract

Aim Our aim was to understand how similarity changes with distance in biological communities, to use the distance decay perspective as quantitative technique to describe biogeographic pattern, and to explore whether growth form, dispersal type, rarity, or support affected the rate of distance decay in similarity.

Location North American spruce-fir forests, Appalachian montane spruce-fir forests.

Methods We estimated rates of distance decay through regression of log-transformed compositional similarity against distance for pairwise comparisons of thirty-four white spruce plots and twenty-six black spruce plots distributed from eastern Canada to Alaska, six regional floras along the crest of the Appalachians, and six regional floras along the east–west extent of the boreal forest.

Results Similarity decreased significantly with distance, with the most linear models relating the log of similarity to untransformed distance. The rate of similarity decay was 1.5–1.9 times higher for vascular plants than for bryophytes. The rate of distance decay was highest for berry-fruited and nut-bearing species (1.7 times higher than plumose-seeded species and 1.9 times higher than microseeded/spore species) and 2.1 times higher for herbs than woody plants. There was no distance decay for rare species, while species of intermediate frequency had 2.0 times higher distance decay rates than common species. The rate of distance decay was 2.7 times higher for floras from the fragmented Appalachians than for floras from the contiguous boreal forest.

Main conclusions The distance decay of similarity can be caused by either a decrease in environmental similarity with distance (e.g. climatic gradients) or by limits to dispersal and niche width differences among taxa. Regardless of cause, the distance decay of similarity provides a simple descriptor of how biological diversity is distributed and therefore has consequences for conservation strategy.

Keywords
Similarity, spatial dependence, distance decay, biological diversity, boreal forest.

INTRODUCTION

The similarity between two observations often decreases or decays as the distance between them increases, a pattern long recognized in the geographical literature and once called 'the first law of geography' (Tobler, 1970). That early interest in the distance decay of similarity led subsequently to formal analyses of spatial autocorrelation and eventually to the field of geostatistics, a field that has grown tremendously in the last decade (Cressie, 1993).

While ecologists and biogeographers have rarely referred to distance decay *per se*, a negative relationship between distance and similarity is implicit in several ecological and evolutionary phenomena. For example, species turnover along spatial environmental gradients produces a decrease of similarity with distance (e.g. Whittaker, 1975; Cody, 1985). Mass effect (Shmida & Ellner, 1984), source-sink dynamics in metapopulations (Hanski & Gilpin, 1991), and supply side ecology (Roughgarden, Gaines & Pacala, 1987) have stressed the importance of dispersal and therefore distance in explanations

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of population dynamics and community composition (Palmer, 1988). Studies in island biogeography have found a decrease in percent species saturation of oceanic or habitat islands as a function of their distance from a source pool of immigrants (Vuilleumier, 1970; Kadmon & Pulliam, 1993), producing a decrease in the similarity of species lists with distance. Dispersal, migration, and gene flow produce geographic patterns in the distribution of genetic variation and in the distribution of species that result from vicariance and adaptive radiations (Meyers & Giller, 1988; Briggs, 1991), leading to spatially autocorrelated distributional patterns that were described in the early biogeographic literature under the age and area and centre of origin hypotheses (Cain, 1944; Willis, 1922).

These examples suggest two very different causes of biological distance decay. On the one hand, a decay of similarity results from a simple decrease in environmental similarity with distance (e.g. movement along a topographic or climatic gradient). In this case, the underlying explanation is competitive sorting of species with different physiological abilities; composition, at least after sufficient time has elapsed, is predictable from environment. We term this source of biological distance decay the niche difference model.

The second cause of distance decay is that the spatial configuration (the size and isolation of habitats), spatial context (the nature of the matrix surrounding the habitats), and time influence species and gene movement across landscapes. Variation in distance decay rates among landscapes occurs in this case because different landscapes have different resistances to the movement of organisms. Variation in distance decay rates among different species groups will also arise if the groups have different dispersal abilities—in essence, different species will perceive a given spatial configuration of habitats differently. Variation in landscape resistance to movement and in dispersal abilities suggest an interaction between the spatial template and time: the greater the resistance to movement or the less vagile the organism, the greater the amount of time required for the organism to cross a given spatial template. As a result, the nature of the spatial configuration of habitats will affect how long the effects of historic events persists in terms of distributional patterns of species. When time or dispersal are limiting, current environmental conditions will not fully explain species distributions or local composition. We term this source of distance decay the model of temporal and spatial constraint: history and the nature of the spatial template explain species distributions. At large scales of space and time, the imprint of past events has been termed historic biogeography (Schluter & Ricklefs, 1993).

In this paper we explore distance decay as a descriptor of compositional variation. We first discuss scale dependence in the detection of distance decay and develop a conceptual framework for distance decay. We then examine distance decay rates in boreal and montane spruce-fir forests, comparing the rate of similarity decay in several species groups (vascular plants, mosses, species abundance classes, growth form classes, and dispersal classes) across the same set of plots. Finally, we discuss the implications of distance decay perspective for community composition, biogeographical pattern, and conservation.

DISTANCE DECAY OF BIOLOGICAL SIMILARITY: CONCEPTUAL FRAMEWORK

Distance decay and geostatistics

Our approach to the distance decay of similarity is parallel to, but methodologically different from, geostatistical approaches to the analysis of spatial autocorrelation (Cressie, 1993). It is now standard practice to use semi-variograms to characterize the relationship of variance of a parameter to intersample distance or lag (Ripley, 1988), a critical step in the optimal interpolation technique called kriging (Burrough, 1986; Webster & Oliver, 1990). To construct a semi-variogram, variance is calculated by comparing values of the parameter at two locations of known distance apart. The statistic we model here, similarity, is a parallel concept to variance in the sense that it results from comparison of two observations from different locations. In our case the observations consist of species lists; similarity is a complex function of the occurrence of many species (Faith, Minchin & Belbin, 1987). By contrast, variance is calculated for univariate factors (e.g. soil pH, rainfall, or abundance of a single species).

Variance and similarity both measure differences between samples and can be modelled as a function of intersample distance. In this paper, we use linear regression to model that relationship. The intercept of this model is similar to the nugget effect (residual intersample variance as distance decreases to zero) in semi-variograms. The shape of the similarity-distance relationship can be examined for evidence of a range and sill which, in semi-variograms are, respectively, the distance at which variance becomes independent of further increases in distance and the amount of variance at that distance. Regression of similarity against distance has the advantage in our case of producing a direct estimate of the rate of distance decay and thus the rate of composition change through space. One of our purposes is to ask whether species with different dispersal types or growth forms show different rates of compositional change.

Scale dependence and distance decay

Grain, extent and related geostatistical concepts
Observations of distance decay will show scale dependence. Ecologists have divided scale into grain and extent (Allen & Hoekstra, 1991; Weins, 1989). Grain, which is similar to the concept of support or resolution in the geostatistical literature (Odland, 1988; Webster & Oliver, 1990; Cressie, 1993), is the contiguous area over which a single observation is made (e.g. quadrat, plot, or pixel). In this sense it is a special case of support, which is defined as an *n*-dimensional volume within which a linear averaged value of a regionalized value may be computed (Olea, 1991). Spatial extent, called area in the geostatistical literature (Cressie, 1993), is the space over which observations are made.

The grain size or support of samples will effect observed similarities, a phenomenon known as the support effect in the geostatistical literature. Consider two areas with identical species lists. If a small quadrat is sampled from each area, species-area relationships dictate that these quadrats will have

only a subset of the possible species and will contain identical species lists only a portion of the time. If we increase grain size, however, species lists will become more complete until, at a grain size that is equivalent to the size of the study areas, all possible species will be contained and the observed similarity will equal the real similarity. If two regions have a similarity greater than zero, small samples, by chance, can have either higher or lower similarity than the real similarity. The distribution of sample scores will vary with the distribution of individuals among species, the spatial pattern of species and individuals, the sampling design, and that component of the species-area relationship that we term the species-grain relationship (Palmer & White, 1994). In general, we expect that the variation in observed similarities among samples will increase as grain size decreases, assuming that the real similarity is a positive value. This effect of change in support or grain size on sample statistics has been well discussed in the geographical literature as the modifiable areal unit problem (Openshaw, 1983). It has generally been found that variation increases as support or grain size decreases.

Although distance decay proposes that similarity decreases with extent, natural periodicities in the environment may cause a lack of distance decay at some scales of observation (Fig. 1). Geostatisticians have treated similar patterns of variance as the problem of non-stationarity (Webster & Oliver, 1990). For example, if extent is only large enough to include a mountain crest and its adjacent valley, distance decay will likely occur as a result of the strong environmental gradient that is present. However, if extent is increased to include the next mountain crest, similarity of community composition will likely increase in relation to the first mountain summit. If extent is increased further still to include a large number of mountain crests and valleys, distance decay will likely re-emerge from either climatic gradients or the presence of dispersal barriers between places with similar environments.

The detection of distance decay requires that the variation due to small grain size or support be less than the variation due to spatial extent. Increasing the grain size or support of a sample will decrease variation, and may allow detection of weak distance decay trends. Alternatively, increasing extent while holding sample grain or support constant may allow identification of distance decay trends because the variation due to distance will be larger than the noise present from small grain size or support. The strongest distance decay relationships should be observed when the variation due to sampling error is minimized (with large sample grains or support) and the variation due to distance decay is maximized (with large sample extents).

A conceptual model for variation in distance decay rates

The rate of distance decay will vary with the strength of environmental gradients and will differ among taxa and between landscapes of different spatial configurations and histories. More formally, we suggest that the rate of decay in biological similarity will be correlated with two characteristics of the environment (environmental distance and the nature of

A. HYPOTHETICAL LANDSCAPE
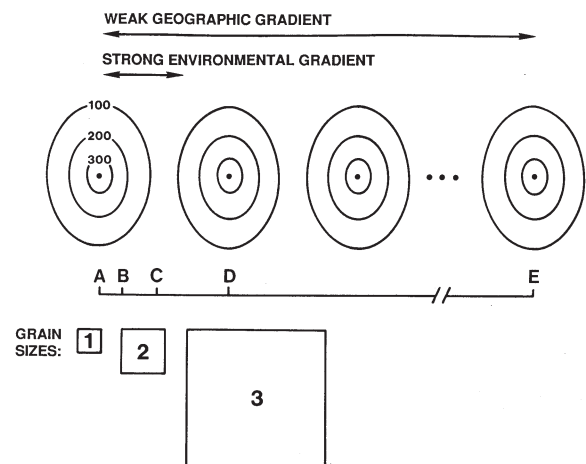
B. SIMILARITY AS A FUNCTION OF GRAIN AND EXTENT
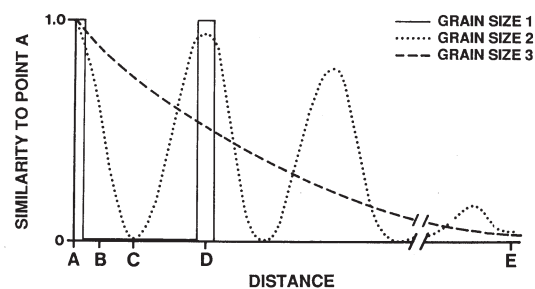
Figure 1 The influence of sample grain and extent on the observation of distance decay. A, A hypothetical landscape with spatial periodicities in similarity controlled by strong environmental gradients (elevation contours); B, the distance decay of similarity as detected by samples of differing grain and extent.

the spatial template) and two characteristics of the organisms under study (niche-breadth and dispersal ability). The effects of each of these factors are discussed below.

Environmental distance

For a fixed spatial distance, the steeper the rate of environmental change, the more rapid the turnover in species composition and the higher the expected rate of distance decay. Ecologists often have assumed that composition is solely a function of environment (e.g. MacArthur, 1972; Tilman, 1988). For the rate of distance decay to be solely controlled by environmental distance, all species must have access to all appropriate habitats and time must be sufficient to allow competitive interactions to sort species as a function of environment. In essence, this summarizes Beijerinck's Law: everything is everywhere but the environment selects (Saur, 1988). Niche characteristics and competition determine composition.

The spatial template

Characteristics of the spatial template (habitat size, isolation, and the nature of the matrix) will effect the rate of distance

decay, all else being equal. The more isolated the habitat, the less efficient dispersal will be. Some species will not locate all available habitats (Huffaker, 1958; Shmida & Ellner, 1984), leading to lower levels of species overlap among sites and higher rates of distance decay. Factors which would effect distance decay rates are: the unfavourability of the matrix (which would affect rates of movement), the favourability of the habitat patches (which would affect size, reproduction, and persistence of the populations), and the presence of corridors or stepping stone connections. In a sense, these measure the resistant to movement of the landscape. The percolation coefficient is an example of a measure of the affect of spatial characteristics on movement. This coefficient represents the permeability of a given landscape to unidirectional organism movement (Gardner et al., 1989).

Niche breadth and overlap
The wider the average niche breadth and overlap for a group of organisms, the lower the rate of distance decay which will occur over a fixed amount of environmental distance. Realized niche breadth and overlap may decrease over successional time as species sort along gradients (Werner & Platt, 1976; Christensen & Peet, 1984).

Dispersal ability
Highly vagile species will be less affected by barriers and will be able to locate most or all of the appropriate habitats in a landscape (Bush & Whittaker, 1991; Dzwonko & Loster, 1992) and such dispersal may compensate for low persistence rates (e.g. as suggested by the source-sink population model and the rescue effect, Brown & Kodric-Brown, 1977). More vagile taxa should therefore show lower rates of distance decay over a given landscape. Species with poorer vagilities will be unable to cross barriers, leading to their absence from potential sites (Weddell, 1991), contributing to higher distance decay rates.

DISTANCE DECAY IN SPRUCE-FIR FORESTS

The boreal and montane spruce-fir forests of eastern and northern North America have similar structures over large areas (Cogbill & White, 1991). Two data sets were constructed from published studies of these forests. In the first, the vascular plants and bryophytes of the North American boreal forests were analysed from data in LaRoi (1967) and LaRoi & Stringer (1976). These papers present species lists for nine hectare plots (300×300 m) distributed from Newfoundland to Alaska in two community types: upland white spruce forests (thirty-four plots containing 252 vascular plant species and 118 bryophyte species) and lowland black spruce forests (twenty-six plots containing 195 vascular plant species and seventy-nine bryophyte species). Similarity and distances were calculated for all pairwise combinations of plots within these two habitat types (a total of 561 values for white spruce stands and 351 values for black spruce stands). These data sets were chosen because they allow us to examine distance decay for relatively homogeneous forests (each of the habitats is dominated by the same tree species throughout) in relatively unbroken topography across a large geographic extent.

The second data set consisted of regional vascular plant lists for the boreal forest and Appalachian montane spruce-fir. While the boreal forest exists in a relatively continuous band from Alaska to Newfoundland, montane spruce-fir is restricted to the highest peaks, with the areas dominated by spruce and fir separated from one another as a series of island-like clusters (Cogbill & White, 1991). Species lists for six boreal and six Appalachian spruce-fir forest regions were compiled from the literature and corrected to a common nomenclatural base (Crandall, 1958; Curtis, 1959; Grigal, 1968; Lakela, 1965; LaRoi, 1967; Maycock, 1961; Maycock & Curtis, 1960; McIntosh & Hurley, 1964; Nicholson, Holway & Scott, 1969; Ohmann & Ream, 1971; Oosting & Billings, 1951; Ramseur, 1960; Siccama, 1974; White, 1982; White & Miller, 1988). Similarity was calculated between all pairwise comparisons of these regions within both groups. This data set has a larger support (each list is a regional flora) than the one from LaRoi (1967).

We addressed several questions using these data sets: Does community similarity decrease with distance and, if so, what statistical model best describes this relationship? Do isolated habitats (Appalachian mountain summits and slopes) have a higher rate of distance decay than more contiguous ones (boreal forest)? Do data sets with larger grain size or support (the regional floristic lists), because they have more complete species lists, have higher overall similarities and lower distance decay rates than data sets with smaller grain size or support (boreal forest plot data)? Do wind-dispersed species (bryophytes and wind-dispersed vascular plants) have higher rates of distance decay than less vagile species? Do taller and dominant species (which may have broader environmental tolerances) have lower distance decay rates than smaller and understory species?

We addressed the questions about dispersal, dominance, and frequency by using data from a single set of plots, thus holding spatial configuration and environmental distance constant for all groups compared. The distance decay rates for bryophytes and vascular plants were compared with data from both white spruce and black spruce plots. Comparisons among vascular plant classes were made with data from white spruce plots only. The following paragraphs describe the questions addressed with white spruce plots in more detail.

The contribution of species in different frequency classes to distance decay rate
Species were divided into three classes: species found on one to three plots (139 species), four to fourteen plots (eighty-four species), and fifteen to thirty-four plots (twenty-nine species). We also summed the last two classes to produce a fourth class, those species found on four to thirty-four plots (113 species). Common species are shared by many plots and therefore decrease the overall rate of distance decay (in the extreme, for species found in all plots, intersample similarity is always 1.0 and is independent of distance). Species found in only one plot would lower the similarity between any two plots but would not contribute to a spatial trend in similarity at this scale (similarity based on these species would be zero at all distances). We therefore hypothesized that species with intermediate frequency would show the steepest rate of distance decay.

Variation in distance decay rate among growth forms
Casual observation suggested that trees in the boreal forest have wider geographic distributions than plants with other growth forms. This suggests wider environmental tolerances and a lower distance decay rate. We therefore investigated whether there were systematic differences in distance decay rates for plants with different growth forms. Species were divided into five classes: trees (nineteen species), tall shrubs (twenty-two species), low shrubs (thirty-five species), subshrubs (sixteen species), and herbs (160 species). We also compared the bryophyte data to the data from these vascular plant growth form classes.

Variation in distance decay rate among dispersal classes
More vagile species should have lower distance decay rates than less vagile species. Species were divided into three major and five total dispersal classes: wind dispersed species (a total of sixty-three species, comprised of two subcategories, twenty-eight spore/microseed species and thirty-five plumose seed species), berry-fruited/nut-bearing species (sixty-four species), and species with other dispersal types (125 species). We also compared the bryophyte data to the data from these vascular plant dispersal classes.

Similarity index
We used Jaccard's Index (Mueller-Dombois & Ellenberg, 1974) due to its simplicity, its widespread use, its accessibility through common statistical packages, and its use of presence/absence data. We chose a presence-absence metric because it represents a more conservative measure of community similarity than ones based on species abundance data which are more sensitive to disturbance and local environmental differences.

Data analysis
For the largest empirical data sets (white spruce and black spruce stands of the boreal forest), similarity and distance were calculated and then log-transformed. Linear regression was used to calculate distance decay rates or all four combinations of these transformed and untransformed variables. Inspection of the plots and regression residuals were used to determine which formulation most closely approximated a linear relationship over most intersample distances.

Because the values in the matrices (561 for white spruce stands, 351 for black spruce stands) are not independent, randomization tests were used to establish the significance of regression models and to make comparisons of distance decay rates among various subsets of the data. Mantel tests with 10,000 replications (Jackson & Somer, 1989) were used to estimate significance of each model (Manly, 1991).

The comparison of distance decay rates among various subsets of the data was done with a randomization test developed by Blake Weiler of the Ecology Curriculum at the University of North Carolina at Chapel Hill. Our objective was to compare the slopes of the distance decay relationship between two data subjects (e.g. trees *v.* herbs) across all plots. The method followed this outline: (1) all non-zero similarities based on the two data subsets to be compared

were assembled (we used non-zero values because we were interested in the slope of the distance decay relationship over those distances that have a measured similarity—presumably similarity falls to zero at some distance and then is independent of distance thereafter); (2) after testing the difference in mean similarity for the two data subsets, similarity values within each subset were rescaled to a common mean (we sought to test the difference in slopes of the distance decay relationships independent of differences in the means); (3) for each pair of sites, the two similarity values (one for each of the two data subsets to be compared) were randomly reassigned to the two data subsets; (4) after this randomization had been carried out for all pairs of sites, linear regression was used to determine the slope of the distance decay relationship for each of the randomized subsets; (5) step four was repeated to produce 10,000 values for the slope of the distance decay relationship for randomized subsets; (6) finally, the absolute difference between the slopes in each of the 10,000 randomizations was compared to the difference between the observed slopes based on the original data (and thus the true assignments to data subset categories) and we calculated how many times (out of 10,000 trials) randomization produced a difference in slope between the subsets that was at least as great as the observed difference in slope based on the original data. If correct assignment to data categories is significant (if the categories are indeed different in slope), then the observed difference should exceed the randomized differences a high percentage of the time. We used this percentage as the *P* value for our tests.

RESULTS

Distance decay in spruce-fir forests

In all data sets except for rare species in white spruce stands, similarity decreased significantly with distance (Figs 2–6, Table 1). The most linear relationship and the most heteroscedastic regression residuals were found in models that used the log transformation of similarity and untransformed distance. A semi-log model was thus used in all of the regression models presented here. This implies an exponential rate of distance decay. For the boreal forest plot data, the rate of similarity decay ranged from -0.17 (black spruce bryophytes; units are in ln (similarity) per 1000 km of distance) to -0.55 (white spruce vascular plants of intermediate frequency) and r^2 values ranged from 0.24 (black spruce bryophytes) to 0.71 (common vascular plants on white spruce plots). For the regional floras, the rate of similarity decay ranged -0.25 (boreal forest, $r^2 = 0.54$) and -0.67 (Appalachian montane forest, $r^2 = 0.80$). All of these relationships are fit well by a straight line in log-linear space (Figs 2–6), with no obvious sill (i.e. no distance at which the data imply a change of slope for the regression). Our closest observations are not close enough for a detailed analysis of the intercept value for the regressions, which is analogous to the nugget effect in semi-variograms, although we make a few comments on that parameter below.
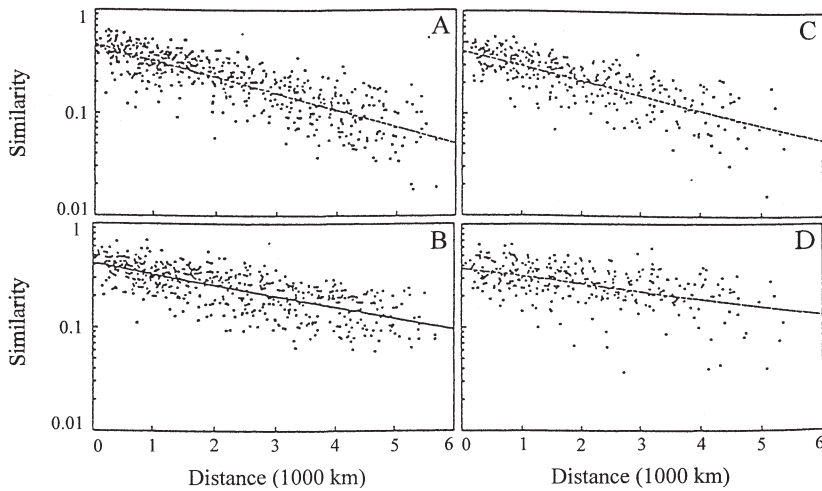
Figure 2 The log of similarity plotted against distance for all pairwise comparisons of plots sampled across the boreal forest based on data in LaRoi (1967) and LaRoi & Stringer (1976). A, Vascular plants in thrity-four white spruce stands; B, bryophytes in thirty-four white spruce stands; C, vascular plants in twenty-six black spruce stands; D, bryophytes in twenty-six black spruce stands.
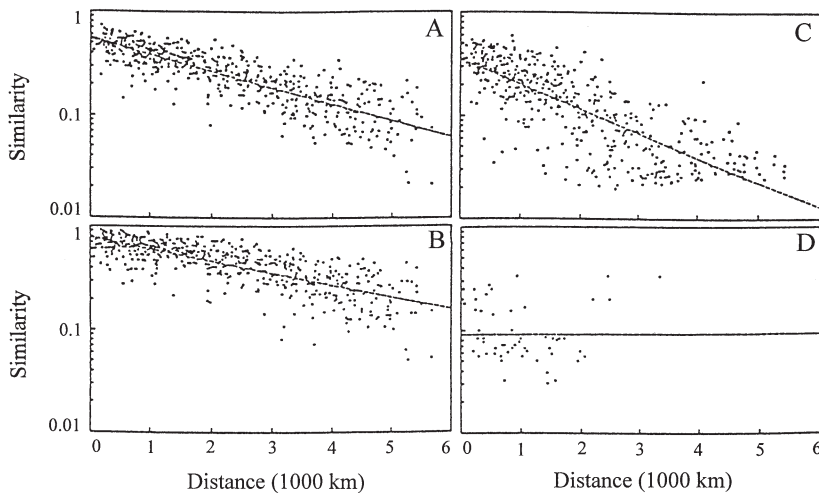
Figure 3 The log of similarity plotted against distance for species frequency classes (white spruce stands only; data from LaRoi, 1967). A, Vascular plants found in four or more plots; B, vascular plants found in fifteen to thirty-four plots; C, vascular plants found in four to fourteen plots; D, vascular plants found in three or fewer plots.

The effect of frequency, growth form, dispersal type, and habitat isolation on distance decay rates

Species frequency
When rare species (those occurring in three or less of the 34 white spruce plots) were eliminated from the data set, the rate of distance decay was unaffected (Fig. 3A; Table 1), but similarities were generally higher, the intercept was closer to unity (complete similarity at a distance of 0), and the r^2 value was higher. Thus, rare species lower overall similarity but do not affect the rate of distance decay. As might be expected from this analysis, the rare species themselves showed no decay of similarity as a function of distance (Fig. 3B).

The species occurring in four or more plots were divided into two groups: common species (fifteen or more plots) and intermediate species (four to fourteen plots). The common species had a higher intercept value than intermediate species and a rate of distance decay (-0.27) that was only one half as great as the rate for intermediate species (-0.55) (Fig. 3C–D; Table 1).

The influence of rare species can also be seen by comparing distance decay rates for regional floras (Fig. 6) with those for plot data (Fig. 2). Both include data taken over the geographic extent of boreal forest, but the floristic lists include rare species that are at their range limits at each location, whereas the plots are less likely to sample species that are very rare in the landscape as a whole. The fuller regional species lists (and larger support) of the floristic data set lowers the observed rate of similarity loss per unit distance. In a sense, the larger support reduces the observed rarity of species. Thus, the rate of distance decay for boreal forest plot data was 1.5 times higher than that for boreal forest floristic lists across the same geographical extent (Table 1).

Growth form
In the white spruce plots, herbs had 1.7–2.1 times higher distance decay rate than woody plant classes ($P < 0.005$–0.0001; Tables 1 and 2, Fig. 4). The higher distance decay rate for the smallest vascular plants was reversed for the contrast between vascular plants and bryophytes: herbs had 1.6 times the rates for bryophytes in the same plots (Fig. 2, Table 1). Interestingly, bryophytes had similar rates of distance decay to tall woody
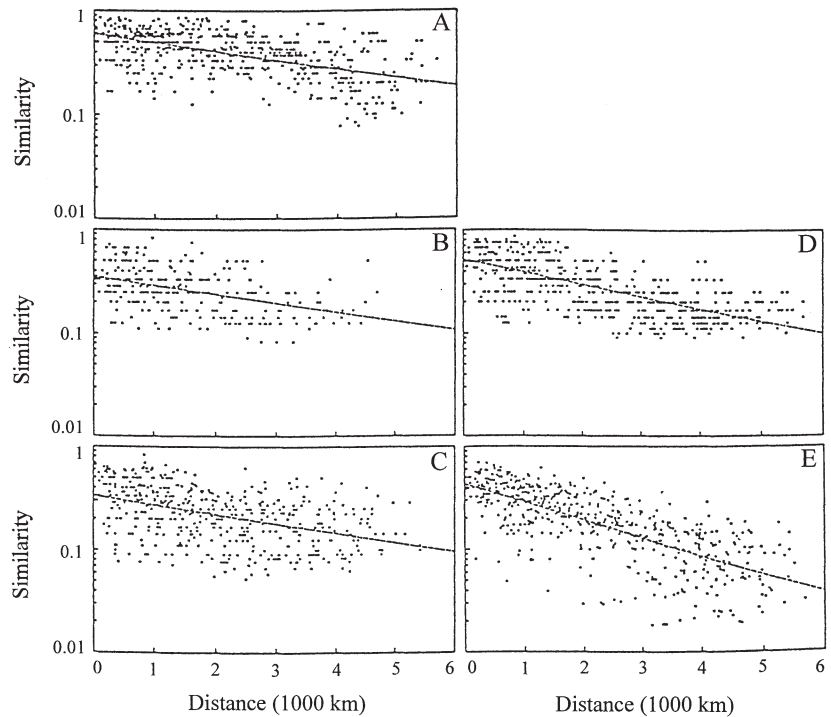
Figure 4 The log of similarity plotted against distance for growth form classes (white spruce stands only; data from LaRoi, 1967). A, Trees; B, tall shrubs; C, low shrubs; D, subshrubs; E, herbs.
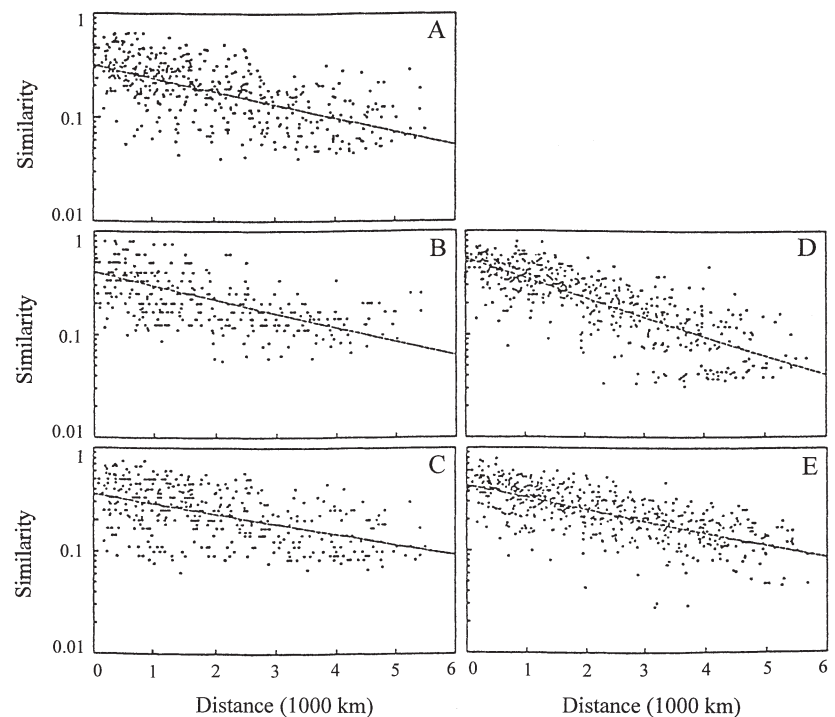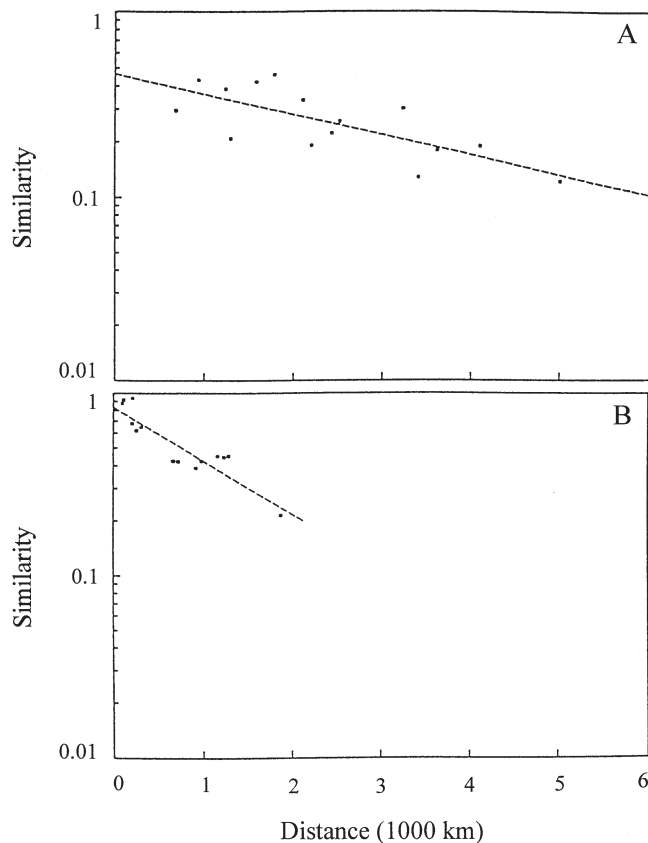

Figure 5 The log of similarity plotted against distance for dispersal classes (white spruce stands only; data from LaRoi, 1967). A, Wind-dispersed species; B, species with plumose seeds; C, species with spores or microscopic seeds; D, species with nuts or fleshy berries; E, species with other types of seeds.

plants on the same plots; they also had similar rates to wind-dispersed vascular plants (see below). Vascular plants as a group had 1.5 (white spruce plots) and 1.9 (black spruce plots) times higher distance decay rates than bryophytes of the same plots (comparisons significant at the $P < 0.001$ level; Table 1).

Dispersal type
For vascular plants on white spruce plots, berry-fruited and nut-bearing species had nearly twice the rate of distance decay shown by spore/microseed and plumose seed species (-0.43 $v.$ -0.23 and -0.25, $P < 0.001$; Tables 1 and 2, Fig. 5B, C, and

Figure 6 The log of similarity plotted against distance for all pairwise comparisons of vascular plant floras from six regions across the northern boreal forest [data modified from Curtis (1959), Grigal (1968), Lakela (1965), LaRoi (1967), Maycock (1961), Maycock & Curtis (1960) and Ohmann & Ream (1971)] and six areas along the crest of the Appalachian mountains [data modified from Crandall (1958), LaRoi (1967), McIntosh & Hurley (1964), Nicholson, Holway & Scott (1969), Oosting & Billings (1951), Ramseur (1960), White (1982)]. A, Boreal spruce-fir forests; B, Appalachian spruce-fir forests.

Data set	Species	n	Intercept	Slope	r^2	P
White spruce vascular plants	252	561	−0.75	−0.37	0.67	0.0001
White spruce bryophytes	118	561	−0.87	−0.25	0.53	0.0001
Black spruce vascular plants	195	351	−0.88	−0.33	0.57	0.0001
Black spruce bryophytes	70	351	−0.98	−0.17	0.24	0.0001
Data subsets (white spruce plots only)						
Frequency class:						
4–34 plots	113	561	−0.57	−0.37	0.71	0.0001
15–34 plots	29	561	−0.24	−0.27	0.59	0.0001
4–14 plots	84	467	−1.04	−0.55	0.66	0.0001
1–3 plots	139	63	−2.40	−0.006	0.00	n.s.
Growth form:						
Trees	19	555	−0.51	−0.19	0.30	0.0001
Tall shrubs	22	271	−1.21	−0.20	0.17	0.0001
Low shrubs	35	472	−1.09	−0.21	0.20	0.0001
Subshrubs	16	528	−0.66	−0.28	0.45	0.0001
Herbs	160	554	−0.84	−0.40	0.52	0.0001
Dispersal class:						
Wind	63	485	−1.14	−0.29	0.38	0.0001
Plumose	35	329	−1.09	−0.25	0.31	0.0001
Spore/microscopic	28	408	−1.02	−0.23	0.28	0.0001
Fleshy fruits, nuts	64	532	−0.62	−0.43	0.62	0.0001
Other	125	561	−0.84	−0.27	0.48	0.0001
Boreal forest regions	250	15	−0.76	−0.25	0.54	0.0039
Appalachian spruce-fir	226	15	−0.18	−0.67	0.80	0.0018

Table 1 Regression statistics for the decay of similarity with distance in spruce-fir data sets. The sample size (n) is the number of similarity values and distances in each matrix. The number of plots or areas are as follows: white spruce plots, 34; black spruce plots, 26; boreal spruce-fir areas, 6; Appalachian montane spruce-fir areas, 6. For the three data subsets of the white spruce plots, the sample size is sometimes lower than 561 because of the removal of plot pairs with a similarity of zero. Intercepts are in units of ln(similarity). Slope values are in units of ln(similarity) per 1000 km distance.

Table 2 Significance levels for differences in slopes for the growth form and dispersal classes.

A. Growth form				
	Tall shrubs	Low shrubs	Subshrubs	Herbs
Trees	0.05	0.05	0.0001	0.0001
Tall shrubs		(0.18)	0.01	0.005
Low shrubs			0.005	0.0001
Subshrubs				0.0001

B. Dispersal class				
	Plumose	Spore/micro.	Fleshy	Other
Wind	(0.0649)	0.0001	0.0001	0.004
Plumose		(0.645)	0.0001	(0.79)
Spore/microseeded species			0.0001	(0.306)
Fleshy fruited, nut-bearing species				0.0001

E). Berry-fruited and nut-bearing species had the highest r^2 values among the dispersal types (Table 1). These data suggest that wind-dispersed species are both more widely dispersed and more variable in their occurrences. Bryophytes had similar distance decay rates to spore/microseeded and plumose seeded vascular plants on the same plots (Table 1).

Habitat isolation
Appalachian forest communities had a rate of similarity decay 2.7 times that observed for the continuous northern boreal forest (Fig. 6, Table 1).

DISCUSSION

Form of the distance decay model

In the geographic literature, a distance effect on the interaction between human populations has been modelled with a power or gravity function (Bennett & Gade, 1979):

$$I = A*d^{-c}$$

where I is interaction, A is a constant, d is distance, and c is the friction coefficient (correlated with technologies for communication and barriers to movement over a given distance). This model implies an ever decreasing effect of a unit distance as distance becomes larger and a linear relationship only under double log transformation.

The finding that a semi-log model showed the most linear relationships suggests similarity could in fact be related to distance through an exponential model:

$$S = S_0 e^{-cd}$$

where S is similarity at distance d; S_0 is initial similarity or similarity at distance 0; c is a constant for the rate of distance decay; and d is distance. Exponential decay models have previously been used in biogeography and ecology to model plant dispersal (Okubo & Levin, 1989) and to describe the relationship between spatial distance and floristic similarity in the Galapagos (Preston, 1962). The exponential model, in contrast to the power model, implies a constant proportional change in similarity per unit distance. This is attractive because it suggests that the processes underlying the distance decay relationship vary only with environmental distance, spatial configuration, and organism attributes but not with distance independent of these factors. Hubbell (1995) has produced a simulation model of species colonization and extinction that results in just such a decrease in similarity with distance.

Variation in distance decay rates

The rate of distance decay varied among species groups in expected ways: on the same plots, spore/microseeded and plumose species had lower rates of distance decay than larger fruited species. Trees, other woody plants, wind dispersed, and more frequent species raised overall similarity and lowered the rate of distance decay, while herbaceous plants, heavy fruited, and less frequent species lowered the rate. Further, the more fragmented montane forests dominated by the same genera of trees as the boreal forest had much higher rates of distance decay than the more contiguous boreal forest itself. We will consider alternative explanations for these patterns.

While it can be suggested that due to their small propagule size bryophytes should be more vagile and possess wider ranges along geographic gradients than vascular plant species (Saur, 1988), other explanations are reasonable. The smaller size of bryophytes compared to vascular plants may allow persistence in microsites not available to vascular plants, thus increasing geographic range. Bryophytes may have broader physiological tolerances and higher persistence rates because they can cycle rapidly between active and dormant states.

In light of these possibilities, it is interesting to note that herbs, which are the smallest vascular plants (thus sharing, with bryophytes, environments that have less fluctuating air temperatures), showed the highest rates of similarity loss with distance of all groups. By contrast, wind-dispersed vascular plants had very similar rates of distance decay to bryophytes on these plots regardless of plant stature. Tall vascular plants had as low or lower distance decay rates than bryophytes.

In terms of the comparison of wind and non-wind dispersed species, dispersal type could be correlated with other traits that

influence the rate of geographic turnover. For example, wind-dispersed species could have wider niche breadth (as has been argued for early successional species generally), thus showing a lower rate of distance decay. On the other hand, wind-dispersed species often have small seeds and may therefore have a lower probability of establishment from a given dispersal event, particularly in undisturbed forest studies here (i.e. the probability of establishment in late successional stands could be correlated with seed size). It is unclear how this would influence distance decay; a simple expectation is that it would tend to make similarity more variable at any distance.

The higher rate of distance decay in the Appalachian montane spruce-fir forests could be due to less efficient dispersal among fragmented habitats, but it could also be the result of history (the southern and northern Appalachian spruce-fir forest may have had access to different refugial populations after climatic warming started 15,000 years BP) and/or steeper rate of environmental change with distance. In terms of environmental distance, montane spruce-fir forests have very similar growing season temperatures across the wide range of latitudes covered in the data set (a mean July temperature of 17°C is correlated with their lower elevational boundaries), but are exposed to increasingly low winter temperatures northward (Cogbill & White, 1991).

Sorting out the relative importance of environment and niche-based explanations from spatial configuration and dispersal-based ones is a difficult challenge. Explanations of species composition based on environmental factors and competition are old ones in ecology. However, explanations based on history and dispersal have also been proposed from the beginning. Gleason (1923) suggested that in the Midwest passive dispersal of propagules was the major factor explaining community composition. Palmgren (1926) found that many plant species of the Åland Archipelago, Finland, were absent from seemingly suitable sites, and suggested that dispersal limitation was responsible for this pattern.

When species do not disperse to all appropriate sites, composition will be constrained by the spatial configuration of sites and dispersal abilities of species. At one extreme (if all species had the same dispersal abilities), community composition would be a stochastic subset of the species which can occupy that habitat. Shmida & Ellner (1984) and Shmida & Wilson (1985) have shown how such conditions may lead to the coexistence of co-competitive species in a landscape, which are allowed to co-exist only because populations are spatially separated from each other at any given moment. At the other extreme (if species have a graded series of dispersal abilities), community composition at each location would be a nested subset (varying with habitat isolation) of the full species list. Hierarchical nesting of species lists has been much discussed in the context of habitat area and area-sensitive species (Patterson, 1987); similarly, there may be isolation-sensitive species. Presences explained not by local environment but by continued dispersal has been termed mass effect (Shmida & Wilson, 1985); here we add that absences can be the result, not of local environment, but of dispersal limitations and of stochastic patterns of original colonizing populations (e.g. the imprint of initial refuge competition and migration routes).

Regardless of whether we can evaluate causes, the decay of similarity with distance is a relatively simple descriptor of variation in species composition and has consequences for how we conserve biological diversity. Whether because of environmental distance decay or spatial and historical factors, the distance decay paradigm suggests a natural world that is, at some scales, everywhere unique. Distance decay rates describe the rate of turnover that underlies this uniqueness.

Simberloff & Abele (1970) argued that the theory of island biogeography was silent on preserve design; that is, this theory could not be used to argue whether one large area would have more species than several smaller areas that summed to the same total area. They suggested that the critical factor was the degree of overlap (i.e. the similarity) among the smaller areas. Shafer (1990) showed that whether one area or several small areas of the same total area had more species or not was dependent on two factors: the slope of the log(species)-log(area) relationship and the similarity among the smaller areas. We add here that if the smaller areas (which are by definition non-contiguous and thus spatially dispersed compared to one contiguous area) are more different from one another as a function of the distance between them (see also Palmer & White, 1994), then the decay of similarity with distance is a central explanation of why some investigators (e.g. Stohlgren & Quinn, 1991) find that smaller dispersed conservation areas collectively have more species than large conservation areas. In essence, conservation strategy requires both grain size for population persistence (Shoenwald-Cox, 1983; Newmark, 1987) and spatial extent (for capturing areas dissimilar to one another). The SLOSS (single large or several small) debate can never be resolved because size (grain) and subdivision (extent) maximize different aspects of how biological diversity is distributed. The distance decay of similarity, in this sense, provides a metric and a conceptual base for such efforts as GAP analysis that seek to identify habitats and species left out of existing conservation areas (Davis et al., 1990).

REFERENCES

Allen, T.F.H. & Hoekstra, T.W. (1991) Role of heterogeneity in scaling of ecological systems under analysis. *Ecological heterogeneity* (ed. by J. Kolasa and S.T.A. Pickett), pp. 47–68. Ecological Studies 86. Springer-Verlag, New York.

Bennett, D.G. & Gade, O. (1979) *Geographic perspectives in migration research*. University of North Carolina at Chapel Hill Department of Geography Studies in Geography, Number 12.

Briggs, J.C. (1991) Historical biogeography: the pedagogical problem. *J. Biogeogr.* **18**, 3–6.

Brown, J. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Burrough, P.A. (1986) *Principles of geographical information systems for land resources assessment*. Oxford University Press, New York.

Bush, M.B. & Whittaker, R.J. (1991) Cracked: colonization patterns and hierarchies. *J. Biogeogr.* **18**, 341–356.

Cain, S.A. (1944) *Foundations of plant geography*. Hafner Publishing Co., New York.

Christensen, N.L. & Peet, R.K. (1984) Secondary forest succession on the North Carolina Piedmont. *Forest succession: concepts and*

application (ed. by D.C. West, H.H. Shugart and D.B. Botkin), pp. 230–245. Springer-Verlag, New York.

Cody, M.L. (1985) Towards a theory of continental species diversities. *Ecology and evolution of communities* (ed. by M.L. Cody and J.M. Diamond), pp. 214–257. Harvard University Press, Cambridge, Mass.

Cogbill, C.V. & White, P.S. (1991) The latitude-elevation relationship for Appalachian spruce-fir. *Vegetatio*, **94**, 153–175.

Crandall, D.L. (1958) Ground vegetation patterns of the spruce-fir area of the Great Smoky Mountains National Park. *Ecol. Monogr.* **28**, 337–360.

Cressie, N.A. (1993) *Statistics for spatial data*. John Wiley & Sons, New York.

Curtis, J.T. (1959) *The vegetation of Wisconsin*. University of Wisconsin Press, Madison.

Davis, F.W., Stoms, D.M., Estes, J.E., Scepan, J. & Scott, J.M. (1990) An information systems approach to the preservation of biological diversity. *Int. J. Geogr. Info. Syst.* **4**, 55–78.

Dzwonko, Z. & Loster, S. (1992) Species richness and seed dispersal to secondary woods in southern Poland. *J. Biogeogr.* **19**, 195–204.

Faith, D.P., Minchin, P.R. & Belbin, L. (1987) Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, **69**, 57–68.

Gardner, R.H., O'Neill, ??, Turner, M.G. & Dale, V.H. (1989) Quantifying scale-dependent affects of animal movement with simple percolation models. *Landscape Ecol.* **3**, 217–227.

Gleason, H.A. (1923) The vegetation history of the middle west. *Ann. Assoc. Am. Geogr.* **12**, 39–85.

Grigal, D.F. (1968) *The relationship between plants communities and soils in northeastern Minnesota*. PhD Dissertation, University of Minnesota, Minneapolis.

Hanski, I. & Gilpin, M. (1991) Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linn. Soc.* **42**, 3–16.

Hubbell, S.P. (1995) Towards a theory of biodiversity and biogeography on continuous landscapes. *Preparing for global change: a midwestern perspective* (ed. by G.R. Carmichael, G.E. Folk and J.L. Schnoor), pp. 173–201. Academic Publishing bv, Amsterdam.

Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia*, **27**, 343–383.

Jackson, D.A. & Somer, K.M. (1989) Are probability estimates from the permutation model of Mantel's test stable? *Can. J. Zool.* **67**, 766–769.

Kadmon, R. & Pulliam, H.R. (1993) Island biogeography: effect of geographical isolation on species composition. *Ecology*, **74**, 977–981.

Lakela, O. (1965) *A flora of northeastern Minnesota*. University of Minnesota Press, Minneapolis.

LaRoi, G.H. (1967) Ecological studies in the boreal spruce-fir forests of the North American taiga. I. Analysis of the vascular flora. *Ecol. Monogr.* **37**, 229–253.

LaRoi, G.H. & Stringer, M.H. (1976) Ecological studies in the boreal spruce-fir forests of the North American taiga. II. Analysis of the bryophyte flora. *Can. J. Bot.* **54**, 619–643.

MacArthur, R.H. (1972) *Geographical ecology*. Harper and Row, New York.

Manly, B.F.J. (1991) *Randomization and Monte Carlo methods in biology*. Chapman and Hall, New York.

McIntosh, R.P. & Hurley, R.T. (1964) The spruce-fir forests of the Catskill Mountains. *Ecology*, **45**, 314–326.

Maycock, P.F. (1961) Botanical studies on Mont St. Hilaire, Rouville County, Quebec. *Can. J. Bot.* **39**, 1293–1325.

Maycock, P.F. & Curtis, J.T. (1960) The phytosociology of boreal conifer-hardwood forests of the Great Lakes region. *Ecol. Monogr.* **30**, 1–35.

Meyers, A.A. & Giller, P.S. (1988) Process, pattern, and scale in biogeography. *Analytical biogeography* (ed. by A.A. Meyers and P.S. Giller), pp. 3–12. Chapman and Hall, New York.

Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. John Wiley and Sons, New York.

Newmark, W.D. (1987) A land-bridge perspective on mammalian extinctions in western North American parks. *Nature*, **325**, 430–432.

Nicholson, S., Holway, J.G. & Scott, J.T. (1969) *A floristic comparison of undisturbed spruce-fir forests of the Adirondacks with four other regions*. Atm. Sci. Res. Center, State U. of N.Y. at Albany. Rept. 92.

Odland, J. (1988) *Spatial autocorrelation*. SAGE Publications, Newbury Park, California.

Ohmann, L.F. & Ream, R.R. (1971) Wilderness ecology: virgin plant communities of the Boundary Waters Canoe Area. *North Central For. Exp. Sta. Rept*. NC-63. St. Paul, Minnesota.

Okubo, A. & Levin, S.A. (1989) A theoretical framework for data analysis of wind dispersal of seeds and pollen. *Ecology*, **70**, 329–338.

Olea, R.A. (1991) *Geostatistical glossary and multilingual dictionary*. Oxford University Press, Oxford, England.

Oosting, H.J. & Billings, W.D. (1951) A comparison of virgin spruce-fir in the northern and southern Appalachian systems. *Ecology*, **32**, 84–103.

Openshaw, S. (1983) *The modifiable areal unit problem*. Concepts and Techniques in Modern Geography No. 38. Geobooks, Norwich, England.

Palmer, M.W. (1988) Fractal geometry: a tool for describing spatial pattern of plant communities. *Vegetatio*, **75**, 91–102.

Palmer, M.W. & White, P.S. (1994) Scale dependence and the species-area relationship. *Am. Nat.* **144**, 717–740.

Palmgren, A. (1926) Chance as an element in plant geography. *Proceedings of the International Congress of Plant Sciences, Ithaca, New York* (ed. by B.M. Duggar), pp. 591–602. George Banta Publishing Company, Menasha, Wisconsin.

Patterson, B.D. (1987) The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* **1**, 323–334.

Preston, F.W. (1962) The canonical distribution of commonness and rarity: parts I and II. *Ecology*, **43**, 185–215; 410–432.

Ramseur, G.S. (1960) The vascular flora of the high mountain communities of the southern Appalachians. *J. Elisha Mitchell Sci. Soc.* **76**, 82–112.

Ripley, B.D. (1988) *Statistical inference for spatial processes*. Cambridge University Press, Cambridge.

Roughgarden, J., Gaines, S.D. & Pacala, S.W. (1987) Supply side ecology: the role of physical transport processes. *Organization of communities: past and present* (ed. by J.H.R. Gee and P.S. Giller), pp. 491–518. Blackwell Scientific, Oxford.

Saur, J.D. (1988) *Plant migration*. University of California Press, Berkeley.

Schluter, D. & Ricklefs, R.E. (1993) Species diversity: an introduction to the problem. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 1–10. University of Chicago Press, Chicago.

Schoenwald-Cox, C. (1983) Guidelines to management: a beginning attempt. *Genetics and conservation* (ed. by C. Schoenwald-Cox, S.M. Chambers, B. MacBryde and W.L. Thomas), pp. 414–446. Benjamin/Cummings Publishing, New York.

Shafer, C. (1990) *Nature reserves: Island theory and conservation practice*. Smithsonian Institute Press, Washington, DC.

Shmida, A. & Ellner, S. (1984) Coexistence of plant species with similar niches. *Vegetatio*, **58**, 29–55.

Shmida, A. & Wilson, M.V. (1985) Biological determinant of species diversity. *J. Biogeogr.* **12**, 1–20.

Siccama, T.G. (1974) Vegetation, soil, and climate on the Green Mountains of Vermont. *Ecol. Monogr.* **44**, 325–349.

Simberlof, D.S. & Abele, L.G. (1976) Island biogeography and conservation practice. *Science*, **191**, 285–286.

Stohlgren, T.J. & Quinn, J.F. (1991) Evaluating the contribution of northern California National Park areas to regional biodiversity. *Proceedings of the Symposium on Biodiversity of Northwestern California*, 226–232.

Tilman, D. (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton.

Tobler, W.R. (1970) A computer movie simulating urban growth in the Detroit region. *Econ. Geogr.* **46**, 234–240.

Vuilleumier, F. (1970) Insular biogeography in continental regions. 1. The northern Andes of South America. *Am. Nat.* **104**, 378–388.

Webster, R. & Oliver, M.A. (1990) *Statistical methods in soil and land resource survey*. Oxford University Press, Oxford.

Weddell, B.J. (1991) Distribution and movement of Columbian ground squirrels (*Spermophilus columbianus* (Ord)): are habitat patches like islands? *J. Biogeogr.* **18**, 385–394.

Weins, J.A. (1989) Spatial scaling in ecology. *Funct. Ecol.* **3**, 385–397.

Werner, P.A. & Platt, W.J. (1976) Ecological relationships of co-occurring Goldenrods (Solidago: Compositae). *Am. Nat.* **110**, 959–971.

White, P.S. (1982) *The flora of the Great Smoky Mountains National Park: an annotated checklist of the vascular plants and a review of previous floristic work*. USDI, National Park Service, Southeast Regional Office, Res./Resource Manage. Rept. SER-55.

White, P.S. & Miller, R.I. (1988) Topographic models of vascular plant richness in the southern Appalachian high peaks. *J. Ecol.* **76**, 192–199.

Whittaker, R.H. (1975) *Communities and ecosystems*. MacMillan Publishing, New York.

Willis, J.C. (1922) *Age and area: a study in geographical distribution and origin of species*. Cambridge University Press, Cambridge.

BIOSKETCHES

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