

The spatial structure of the physical environment

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Abstract. There is substantial environmental variance at small spatial scales (1 m or less) in both natural and disturbed environments. We have investigated the spatial structure of physical variables at larger scales (up to 10^6 m). We analysed surveys of edaphic properties of Wisconsin forest soils, of the water chemistry of lakes in Ontario and Labrador, and of temperature and precipitation in northeastern North America. We found no clear indication that the variance among sites approaches some maximal value as the distance between them increases. We suggest instead that the variance of the physical environment tends to increase continually with distance. The slope of the log-log regression of variance on distance provides a means of comparing the heterogeneity of different environments with respect to a given factor, or of comparing different factors within a given environment. This slope provides a useful measure of environmental structure that can be related to the biodiversity or plasticity of native organisms.

Key words: Environmental variance – Physical habitat heterogeneity – Spatial scales

Within any given tract of land, individual organisms experience differing conditions of growth: all environments are heterogeneous to a greater or lesser extent. This heterogeneity can be expressed as the environmental variance of some parameter of interest, and estimated by calculating the variance of measurements made at different locations within a defined area. The rate at which environmental variance increases with the distance between sampling locations represents an ecologically relevant measure of environmental structure. If nearby locations are correlated, variance will tend to increase with distance and the likelihood of an organism encountering a different environment as it moves away from its present location will increase; the same rule applies in

principle to progeny dispersed away from their parent. In uncorrelated environments the variance among locations will not change with their distance apart; while there may be environmental variance in the sampled area, the best estimate of environmental condition at different locations within the area will then be simply the mean site environment. Scientists in several disciplines have studied such relationships between variance and distance in spatially organized environmental data (e.g. Journel and Huijbregts 1978; Trangmar et al. 1985; Webster 1985; Meentemeyer 1989), and their geostatistical techniques have recently begun to be imported into ecology (e.g. Fortin et al. 1989; Wiens 1989; Sugihara and May 1990; Borcard et al. 1992), where they are attracting an increasing amount of interest (e.g. Shorrocks and Swingland 1990; Kolasa and Pickett 1991; Levin 1992).

Physical factors often vary substantially at small spatial scales, within areas that would be classified as single habitats. Surveys of cultivated fields have often reported small-scale variation in soil properties; for example, Webster and Butler (1976) found that most of the variance of soil phosphorus within fields occurs within 5 m, and Beckett and Webster (1971) concluded that 1m^2 plots encompass much of the within-field variance for many soil variables. Such results are particularly striking because the effect of most agricultural practices is to homogenize soils and thus remove the variation between nearby sites. In abandoned fields, Tilman (1982) and Robertson et al. (1988) have shown that levels of important soil nutrients vary at a scale of metres, and the relevance of small-scale heterogeneity to plant growth has been confirmed by implant bioassay (Antonovics et al. 1987). Similar patterns have been found in second-growth and managed forests by Palmer (1990), Bringmark (1989) and Boerner and Koslowsky (1989). Very small-scale variation in the concentration of dissolved organic nutrients has even been found in surface waters of the sea (Smith 1986) and in experimental aquatic microcosms (Lehman and Scavia 1982). Surveys of soil variables in an old-growth hardwood forest at Mont

St-Hilaire in southern Quebec have confirmed that an undisturbed natural environment has detectable spatial structure at a scale of metres or less. Within a 50 m × 50 m area of forest floor, variance increased with distance both for abiotic factors such as nitrogen, potassium and pH (Lechowicz and Bell 1992), and for biotic factors integrated by the growth of plants in soil cores extracted from this area (Bell and Lechowicz 1992). Moreover, native plants showed substantial environmental variance at this scale when seeds were put at random back into the area from which their parents were taken (Bell et al. 1992). We conclude that there is substantial and ecologically important environmental variance at scales of a metre or less within cultivated, disturbed and natural environments.

Within areas which are substantially larger than these small experimental plots, we expect to find that the environmental variance is still greater. That is, we expect that environmental variance will increase with the distance between sampling locations, at least over some spatial scales. This is in accord with the widely held view among ecologists that larger areas will subsume a greater range of different environments or habitats. This view was made explicit, for example, in the rationale for the logarithmic increase in the number of species with increasing area that is at the foundation of the theory of island biogeography (MacArthur and Wilson 1967). It is conceivable, however, that the variance of an environmental measure will asymptotically approach some maximum value, so that it remains essentially constant at large distances. There would then be some characteristic scale, above which the environment could be regarded as being randomly structured – greater or lesser distances at these larger scales would not affect the probability of encountering different environmental conditions. Many ecologists would assume that scales approaching the extent of a distinctive habitat or community type would have such an asymptotic variance relationship, and that greater variance would only arise at still larger scales that encompassed additional, novel habitats or communities. In this view, environmental variance across an extensive range of spatial (or temporal) scales would be structured as a series of plateaus of stable variance linked by changing variance at intervening scales. We question this view and suspect instead that environmental variance increases indefinitely with distance (or over time), so that environments can be regarded neither as uniform at small spatial scales nor as random at large spatial scales. This is the possibility that we investigate in this paper, by analysing a variety of spatial data at relatively large scales of up to 10⁶ m.

Materials and methods

We analysed four data-sets that characterized environments at known locations over relatively large spatial and temporal scales: an inventory of edaphic variables in forest soils throughout the state of Wisconsin, the water chemistry of lakes in the Canadian province of Ontario and in the Labrador region of the province of Newfoundland, and for climate at both Canadian and US stations throughout northeastern North America.

Wisconsin forest soils

We obtained a survey of forest soils in Wisconsin from the Wisconsin Plant Ecology Laboratory, Department of Botany, University of Wisconsin, Madison, Wisconsin, USA (Umbanhowar 1990). This included observations at about 1400 sites originally studied as a basis for Curtis' (1959) comprehensive *Vegetation of Wisconsin*; we used data on soil chemistry in the A₁ horizon of forested sites, which was available for about 250–450 sites for different variables. Data values (in their original units, Umbanhowar 1990) were transformed so as to give approximately Normal frequency distributions: log(base 10) for water-retaining capacity, phosphorus, potassium and total nitrogen; square-root for calcium; no transformation for pH. The data were analysed by calculating the variance of all pairs of sites separated by the same distance, in terms of distance classes of equal extent on a log scale. We then expressed the relationship between variance and distance by plotting log variance on log distance. Distance classes with fewer than 50 observations were dropped from the analysis. Although the sampled sites cover the entire state, sites did tend to be somewhat more clustered in certain regions, e.g. in the vicinity of Madison, or near the Trout Lake field station in northern Wisconsin. Removal of these more densely sampled localities from the analysis did not change the shape of the variance plot appreciably, and plots within each cluster resembled plots for the state as a whole. Because all pairwise combinations of sites are used, each site contributes to the estimates of the variance in several different distance classes, and these estimates are therefore not independent of one another. To construct a null model against which the observations could be compared, the observed values of a given variable were assigned randomly to sites, and this randomized data then analyzed in the same way as the actual observations. By repeating this procedure 100 times, the sampling variance of the estimates of the regression coefficient around their expected value of zero could be estimated and used to evaluate the probability that the observed value of the regression coefficient differed from zero by chance alone.

Ontario and Labrador lakes

We obtained data on water chemistry, morphometry and fish diversity for about 10,000 lakes in Ontario from the Ontario Ministry of Natural Resources and Ministry of the Environment, Ottawa, Ontario, Canada. Our analysis is restricted to the set of 1236 lakes with complete data for the variables we analysed: dissolved organic carbon, pH, aluminium, conductivity, lake surface area and mean depth. All except pH were Normalized by log transformation. The analysis then proceeded as for the Wisconsin soils data-set. A smaller data-set for 130 lakes in Labrador was obtained from Scruton (1984). We analysed the same chemical variables as for the Ontario lakes.

Weather in northeastern North America

We obtained daily records of precipitation and temperature from weather stations in northeastern North America from the Canadian Atmospheric and Environment Service and from the National Oceanic and Atmospheric Administration of the United States Department of Commerce. We selected the 50 weather stations (14 in Canada, 36 in the USA) with an unbroken series of records for the 30 years 1951–1980, distributed over an area from the Atlantic coast inland to Thunder Bay, and from the St. Lawrence valley southwards to Georgia. For each station, in each year, we calculated the length of the frostfree period and the average daily precipitation during this growing season. We then analysed these two variables in the same way as the data for soils and lakes, obtaining a separate plot of log variance on log distance for each of the 30 years.

Results and discussion

Wisconsin forest soils

The variance plots for Wisconsin forest soils are shown in Fig. 1. The detailed shape of the plots, and the amount of scatter around the main trend, appear to differ among the variables, although the lack of independence of the estimates for distance classes make it difficult to evaluate the significance of these differences. Samples from different sites were often taken in different years, so that the

Table 1. Randomization tests of the variance plots for Wisconsin forest soils. Observations in each data set are allocated to sites at random and the unweighted slope of the variance plot calculated for the randomized data after discarding distance classes with fewer than 50 observations; 100 replicate independent randomizations yield in each case a mean value close to zero and a standard deviation s_b . The value of s_b is used to evaluate the probability that the estimate of the unweighted least-squares regression coefficient b obtained from the actual data differs from zero by chance alone

Factor	N	b	s_b	$P(b=0)$
Total Nitrogen	330	+0.944	0.0384	$P < 0.001$
Water-retaining Capacity	245	+0.347	0.0456	$P < 0.001$
Calcium	436	+0.249	0.0164	$P < 0.001$
pH	492	+0.180	0.0215	$P < 0.001$
Phosphorus	338	+0.071	0.0230	$P < 0.01$
Potassium	453	+0.071	0.0491	$P > 0.1$

detailed shape of a plot may reflect particular combinations of circumstances of little general interest. However, in all cases there was a tendency for variance in an environmental variable to increase with distance, and except for potassium this tendency seems unlikely to be caused by chance alone (Table 1). There is therefore a consistent tendency for the variance of these edaphic factors to increase over distances between about 2.5 km and 250 km. Moreover, there is no clear and consistent indication that variance approaches an asymptote within this range of distances. In some cases (nitrogen and potassium) there is no demonstrable increase in variance beyond a certain distance, but in other cases (pH and water-retaining capacity) the reverse is true, with variance increasing more steeply at greater distances; the variance of phosphorus and calcium appears to increase at about the same rate over the entire range of distances.

Ontario and Labrador lakes

The variance plots for Ontario and Labrador lakes are shown in Fig. 2 and 3 respectively. They seem to display the same properties as the plots for Wisconsin soils: detailed differences in shape, but a consistent tendency for variance to increase with distance, giving no clear indication that environmental variance reaches an asymptote at distances of between 2 km and 1000 km.

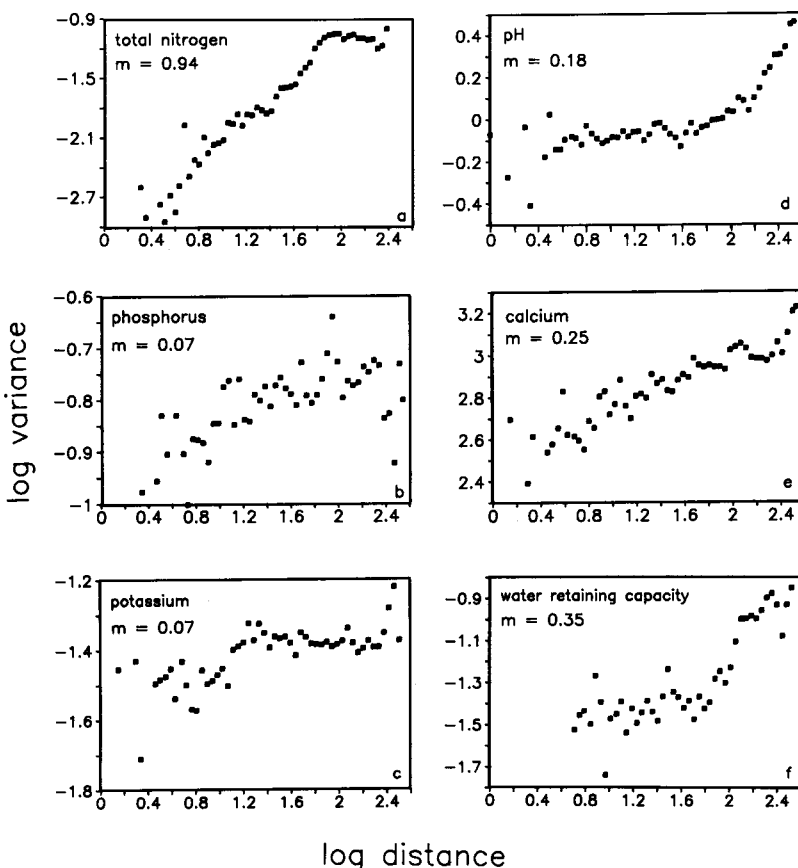


Fig. 1. Large-scale environmental heterogeneity. Figures 1–3 are variance plots in which log variance is plotted on log distance (km) at equally-spaced log distance classes. The data are first normalized and sorted into equal logarithmic distance classes. Estimates based on fewer than 50 pairs of sites are not shown. Regression summary statistics are the slope b of the weighted least-squares regression (unweighted slopes m are cited on the figures), and the proportion of variance attributable to the regression r^2 . Tests of significance are given in Table 1. This figure shows data for Wisconsin forest soils. *a*, Wisconsin total nitrogen ($N=330$, $b=+0.834$, $r^2=0.83$). *b*, Wisconsin phosphorus ($N=338$, $b=+0.025$, $r^2=0.026$). *c*, Wisconsin potassium ($N=453$, $b=+0.048$, $r^2=0.18$). *d*, Wisconsin pH ($N=492$, $b=+0.331$, $r^2=0.70$). *e*, Wisconsin calcium ($N=436$, $b=+0.193$, $r^2=0.71$). *f*, Wisconsin water-retaining capacity ($N=245$, $b=0.514$, $r^2=0.74$).

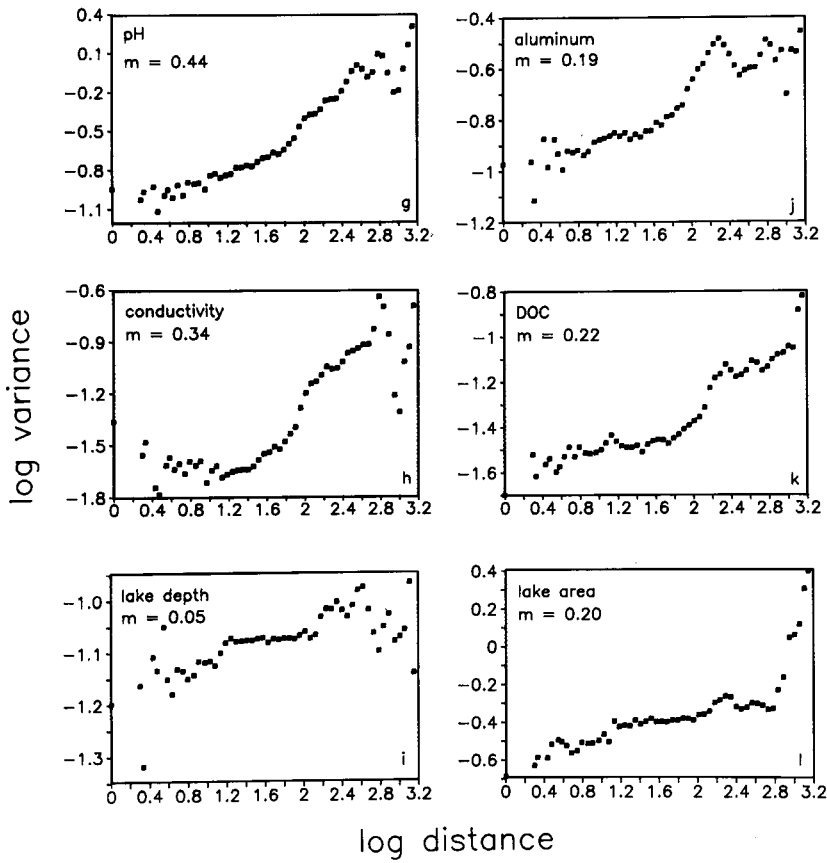


Fig. 2. Variance plots for Ontario lakes (N=1236 lakes). *g*, Ontario pH ($b = +0.545, r^2 = 0.88$). *h*, Ontario conductivity ($b = +0.508, r^2 = 0.77$). *i*, Ontario lake depth ($b = 0.165, r^2 = 0.40$). *j*, Ontario aluminium ($b = +0.181, r^2 = 0.59$). *k*, Ontario dissolved organic carbon ($b = +0.288, r^2 = 0.88$). *l*, Ontario lake area ($b = +0.025, r^2 = 0.10$)

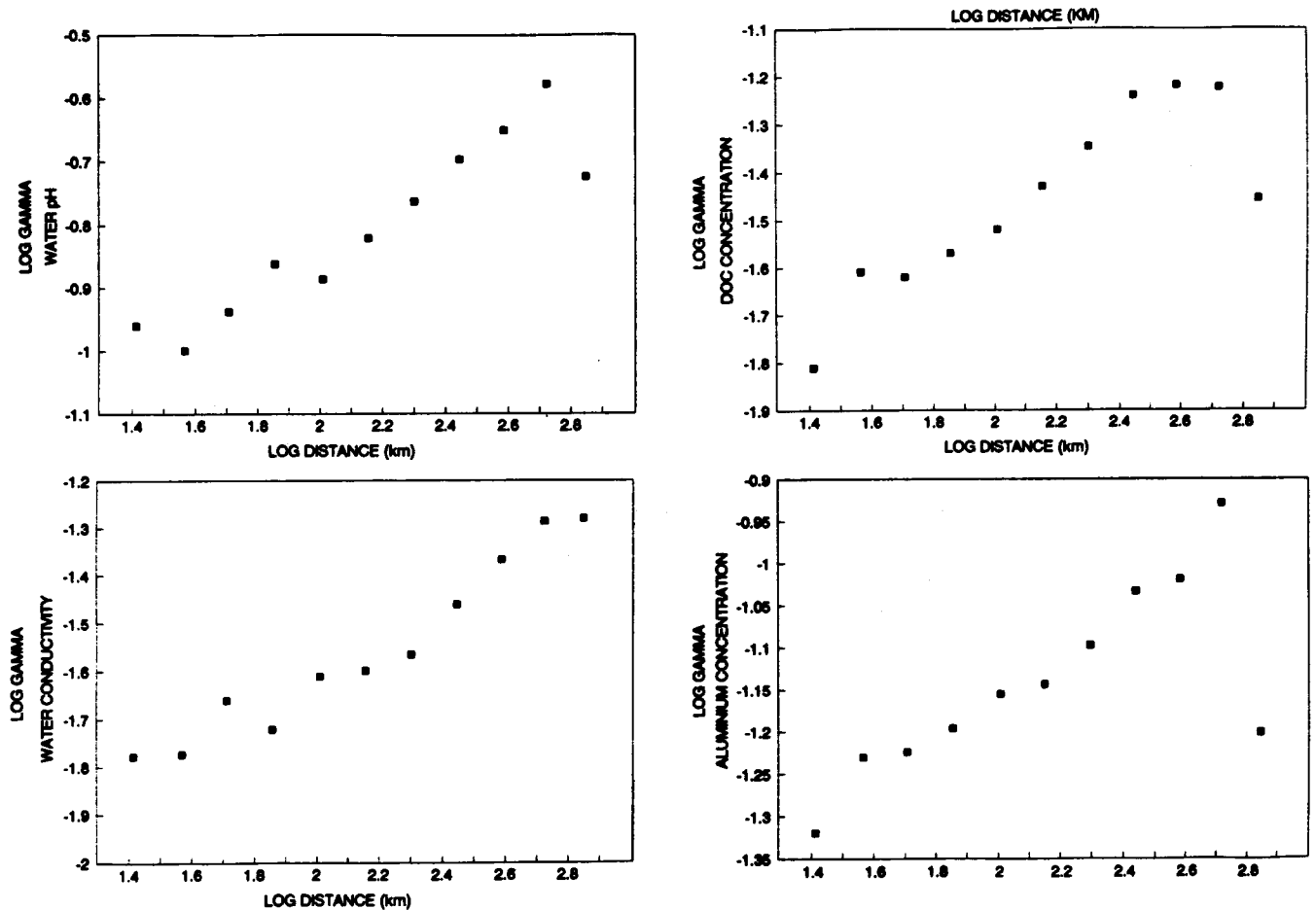


Fig. 3. Variance plots for Labrador lakes (N=130 lakes). *m*, Labrador pH ($b = +0.346, r^2 = 0.94$). *n*, Labrador dissolved organic carbon ($b = +0.447, r^2 = 0.89$). *o*, Labrador conductivity ($b = 0.424, r^2 = 0.90$). *p*, Labrador aluminium ($b = 0.262, r^2 = 0.87$)

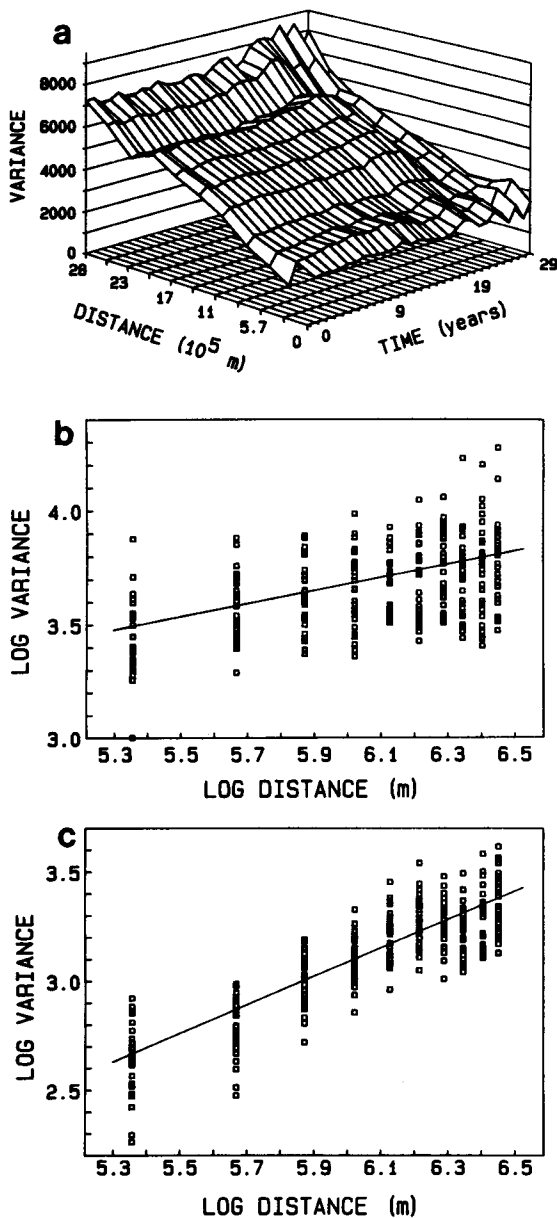


Fig. 4a-c. Variance plots of weather data for northeastern North America. Data from 50 weather stations over 30 years. *a* spatiotemporal variance plot for average daily precipitation. *b* spatial variance plot for average daily precipitation, years plotted separately; regression of means has $b = +0.29$, $r^2 = 0.96$. *c* spatial variance plot for frost-free period, years plotted separately; regression of means has $b = +0.65$, $r^2 = 0.96$

Weather for northeastern North America

The variance of average daily precipitation in space and time is shown in Fig. 4a. Regardless of the time-interval separating measurements, there is a tendency for variance to increase over all spatial scales, up to 2800 km. There is also a much weaker tendency, not analysed here, for variance to increase with separation in time, regardless of spatial location. The spatial variance plots vary in shape from year to year, doubtless as the result of particular combinations of circumstances. However, the availability of 30 years of records makes it possible to

investigate the way in which variance increases with distance on average, over a long series of years. These plots are apparently linear, both for average daily precipitation (Fig. 4b) and for the length of the frost-free period (Fig. 4c), with no indication that an asymptote is approached. We have confirmed that similar analyses of related variables (date of last spring frost; date of first fall frost; total annual precipitation) yield the same result.

General conclusions

In any particular instance, the variance plot shows irregularities which might reflect the spatial structure of a given region, with respect to a defined environmental variable, and which may differ from year to year. However, in all the cases that we have investigated there is a tendency for variance to increase with distance, from distances of less than 10 km to distances of more than 1000 km. Sayles and Thomas (1978) demonstrated a similar rule with respect to the topography of various natural and artificial surfaces. Since this applies to forest soils, to lakes and to weather conditions, we suggest that it may be a general feature of the physical environment. We have not discovered any clear indication that environmental variance approaches an asymptote within this range of distances. It is well known that sampling along an environmental gradient, with the value of a variable increasing monotonically in one direction, will yield variance plots that increase continuously over the range of distances sampled. For example, latitudinal variation may contribute to the variance of the length of the growing season (Fig. 4c). However, it is difficult to accept that monotonic trends extending over the whole range of distances sampled can explain the patterns shown by forest soils and lake waters. The variance of pH tends to increase with distance in Wisconsin forest soils and in Ontario and Labrador lakes, over spatial scales of less than 10 km to more than 1000 km. Lechowicz and Bell (1992) show that there is a tendency for the variance of soil pH to increase with distance at spatial scales of between 10 cm and 10 m in an undisturbed natural forest. Furthermore, Bell (1992) has shown that these patterns are part of a general tendency for the variance of soil pH to increase with distance over 8 orders of magnitude, from 10 cm to 10,000 km, with no indication that an asymptote is approached at any intermediate scale. We are therefore unable to refute the hypothesis that the variance of the physical environment increases indefinitely with distance. We suggest that, as a first approximation, this simple power law offers a robust, general description of the scale-dependent variation ubiquitous in the physical environment and directly relevant to ecology.

Relation to alternative measures

The use of the slope of a variance plot as a general measure of environmental structure has direct affinity with other techniques used in a number of disciplines.

Burrough (1981), for example, identified the slope of the variance plot with the fractal dimension of the environment, and a number of ecologists (e.g. Krummel et al. 1987; Milne 1988; Palmer 1988) have argued the utility of the fractal dimension in the context of community ecology. The semivariogram used in geostatistics (see Webster 1985 and Tringmar, Yost and Uehara 1985 for the use of semivariograms in the analysis of spatial variation in soil properties) is an alternative plot of variance on the scaled separation of sample points, differing only in the definition of a semivariance as opposed to usual formulation of variance. Semivariance suits the statistical requirements for optimal interpolation of values in sparsely sampled spatial or temporal grids; while the *raison d'être* for semivariograms lies in the geostatistics of such kriging exercises, semivariance seems an unnecessary complication for our purposes. A simple plot of log variance on log distance provides a more straightforward and generally useful summation of the way environment changes with scale.

Ecologists have also drawn on a second group of methods for illustrating and analyzing spatial and temporal patterns across a range of scales. These are the methods of spectral analysis (e.g. Platt and Denman 1975; Legendre and Demers 1984), that build on autocorrelations across different scales. Autocorrelation, which is ecologically useful in its own right (Sokal and Oden 1978), emphasizes the relationships among points located relative to one another in time or space; autocorrelation can be employed to evaluate quantitatively the scale-dependence of environmental similarity and difference. Autocorrelational analyses provide a graphical summary of such scale-dependence that can be useful in interpreting the ecological or genetic substructure of populations. Spectral methods extend the autocorrelational approach and seek to isolate an underlying pattern in a spatial or temporal sequence (the "signal") from random noise, usually by decomposing scale-dependent environmental pattern as a sum of harmonic contributions to pattern at different scales. These analyses, which assume an additive linear structure underlying variation across scales, allow autoregressive prediction of conditions or events beyond the range of the sampled data. Such autoregressive predictions can be useful in ecology, especially in the analysis of seasonality and similar repeated temporal patterns.

To some degree the purpose, or at least the ecological use, of spectral methods differs from that underlying the variance plot. The variance plot seeks only to describe quantitatively the degree of variation in the environment likely to be encountered at greater distances or over longer time spans; we argue that the slope of the variance plot can be used for many purposes without further embellishment as a means of expressing this key aspect of environmental structure. Spectral analyses, in contrast, are more often concerned with predicting the actual state of the environment at some distance in space or time. When spectral methods are employed to describe scale dependency, they bring in much detail that is useful in forecasting but has limited biological interpretability. For example, Williamson (1988), following Steele (1985),

referred to the reddened spectrum of environmental variance, the idea that at time scales longer than about 50 years the power spectrum of environmental variance shifts from the white noise of random variation to greater dominance by long ("red" by analogy to light) time spans ("wavelengths"). Despite its attractive imagery, this analogy carries little directly useful quantitative information suited to an ecological or evolutionary analysis. We know only that variation at long time scales is important, but not how that might translate into the probability of an organism or its progeny encountering environmental differences in time or space. Forecasting based on a spectral analysis could address that issue in a particular instance, but the power spectrum itself is a more abstruse and less generally useful summary of the scale-dependence of environmental variation than the simple slope of the variance plot.

Ecological implications

The slope of the variance plot can be used for two main purposes, to investigate whether and to what extent environments differ in structure with respect to some given factor, and, for a given environment, to establish whether factors have different spatial structures. In either case, the slope, as a measure of the spatial structure of the environment, can be used to predict the evolution of genetic diversity and phenotypic plasticity towards different factors or in different environments.

For example, total soil nitrogen ($b = +0.83$) and calcium ($b = +0.19$) appear to behave quite differently in Wisconsin forest soils. A steep slope indicates a coarse-grained environment in which nearby sites are highly correlated, so that dispersing offspring are likely to encounter conditions of growth, with respect to a defined factor such as nitrogen concentration, which are similar to those experienced by their parents. Selection will tend to favour specialization, and over a wide area the population will comprise a diversity of genotypes, each superior over part of the range of environments but inferior to rival specialists elsewhere. A shallow slope indicates a fine-grained environment in which nearby sites are poorly correlated, so that offspring are likely to grow in conditions which differ from those experienced by their parents, with respect to a factor such as calcium. Selection will then tend to favour plasticity, in the sense of possessing the ability to adjust physiologically to any of a range of conditions of growth, in such a way as to maintain a stable level of reproductive success. Organisms may thus be specialized with respect to some factors and plastic with respect to others, or specialized in some environments but plastic with respect to the same factor in others.

The relationship between the variance plot and the response of organisms to environmental heterogeneity can be investigated by growing clones or families of native plants over a range of values of some environmental factor which approximates the range found in nature. A plastic genotype has a low environmental variance for reproductive success. We therefore expect the environmental variance of reproductive success with re-

spect to a given factor to be positively correlated with the slope of the variance plot for that factor in the sites from which the experimental material was collected, when a number of different factors are compared. For example, the native herbs of Wisconsin forests should display greater plasticity with respect to calcium than with respect to nitrogen; in the sense that the average environmental variance of reproductive success should be less among test environments which differ in calcium concentration, and greater among a comparable range of test environments which differ only in nitrogen concentration. The plot of performance on the value of a given environmental factor is a norm of reaction. This plot may sometimes be linear, over the range of values present in the environment. We then expect there to be a positive relationship among different environmental factors between the slope of the variance plot for the environment and the slope of the reaction norm.

Organisms can adapt to particular sites, but they cannot adapt to particular years, although genetic recombination has sometimes been interpreted as a device to preadapt offspring to an uncertain future. Temporal variation should therefore lead to selection favouring phenotypic plasticity, rather than maintaining genetic diversity. The relative importance of spatial and temporal variation of the environment is not known. The variance of precipitation rises more steeply in space than with time in the particular example shown in Fig. 4a, but this is not necessarily a general rule. Localities and years contribute about equally to the variance of agronomic characteristics in crop plants (Bell 1992). Thus, the balance between specialization and plasticity will depend both on the slope of the variance plot in space, and on the relative values of the variance plots for space and time, with a shallow slope and a preponderance of temporal variation favouring plasticity.

Natural selection will lead to adaptation, whether through specialization or through plasticity. Native plants growing in situ will have evolved so as to accommodate environmental heterogeneity, because individuals can tolerate a wide range of conditions, because several specialized genotypes may exist within a species, or because different species have different ecological specializations. Biotic variables such as stand density or productivity will therefore vary less than the underlying physical variables which influence plant growth. We expect the slopes of variance plots to be less for biotic than for physical variables. Moreover, biotic variables may display different patterns in space: we have no reason to suppose that they will tend to increase indefinitely with distance, as physical variables seem to do. There is evidence that the variation in biotic variables like local population size may increase with time (Pimm and Redfearn 1988). The implications for biotic variables of spatial and temporal structure in the physical environment deserves substantially more study than it has yet received.

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