# THE COMPARATIVE EVIDENCE RELATING TO FUNCTIONAL AND NEUTRAL INTERPRETATIONS OF BIOLOGICAL COMMUNITIES

GRAHAM BELL,<sup>1,2,4</sup> MARTIN J. LECHOWICZ,<sup>2</sup> AND MARCIA J. WATERWAY<sup>3</sup>

<sup>1</sup>Redpath Museum, McGill University, 859 Sherbrooke Street West, Montreal, Quebec H3A 2K6 Canada <sup>2</sup>Biology Department, McGill University, 1205 ave Dr Penfield, Montreal, Quebec H3A 1B1 Canada <sup>3</sup>Department of Plant Science, Macdonald College, McGill University, Ste-Anne-de-Bellevue, Quebec H9X 3V9 Canada

*Abstract.* Neutral and functional theories provide rival interpretations of community patterns involving distribution, abundance, and diversity. One group of patterns describes the overall properties of species or sites, and derives principally from the frequency distribution of abundance among species. According to neutral theory, these patterns are determined by the number of individuals of novel type appearing each generation in the community, whereas functional theory relates them to the distribution of the extent of niches. A second group of patterns describes the spatial attributes of communities, and derives principally from the decay of similarity in species composition with distance. Neutral theory interprets these patterns as consequences of local dispersal alone, whereas the functional interpretation is that more distant sites are likely to be ecologically different. Neutral theory often provides good predictions of community patterns, yet is at variance with a wide range of experimental results involving the manipulation of environments or communities. One explanation for this discrepancy is that spatially explicit models where selection is generally weak, or where selection acts strongly on only a few species at each site, have essentially the same output as neutral models with respect to the distribution of abundance and the decay of similarity. Detecting a non-neutral signal in survey data requires careful spatial or phylogenetic analysis; we emphasize the potential utility of incorporating phylogenetic information in order to detect functional processes that lead to ecological variation among clades.

*Key words: abundance; comparative method; distribution; drift; ecological specialization; heterogeneous environment; local adaptation; neutral model, niche, range; spatial ecology; species diversity.* 

## INTRODUCTION

A functionally undifferentiated community in which no novel type ever appears will suffer an irreversible loss of diversity through time, until at last it comprises a single type. In most communities, however, novel types will be generated continually, either by intrinsic processes of genetic change involving residents or by extrinsic processes of immigration from other communities. Diversity is then maintained through stochastic drift as a dynamic equilibrium between the extinction of resident types and the appearance of new ones. Consequently, the amount of diversity that is present at equilibrium can be calculated from the rate of extinction or local extirpation set against the number of individuals of novel type that enter the community in each generation. The generation of novel types is often expressed as the product of two numbers, the first representing the number of individuals in the community, N, and the second the rate at which novel types arise, v, where v might stand for mutation, speciation, or immigration; the dynamics of diversity are then gov-

Manuscript received 16 June 2004; revised 13 December 2004; accepted 4 January 2005. Corresponding Editor: M. Holyoak. For reprints of this Special Feature, see footnote 1, p. 1368.

<sup>4</sup> E-mail: Graham.bell@mcgill.ca

erned by  $N \times y$ . Neutral theory has been developed most thoroughly in population genetics (Kimura 1983), where it has been used to interpret patterns of molecular variation within populations (reviewed by Lewontin 1974, Fay and Wu 2001). It can be applied with equal force to any set of independently replicating entities, whether these are genes, genotypes, or species. Thus, a neutral theory of community ecology, derived from the proposition that individuals are nearly equivalent regardless of the species to which they belong, runs parallel to a neutral theory of population genetics, in which copies of a gene are nearly equivalent regardless of their allelic state.

A functionally differentiated community in which individuals vary in fitness according to their identity is acted on by selection. The effect of selection on diversity depends on its intensity, which can be expressed as a selection coefficient *s*, representing the loss or gain of fitness relative to some standard type. If  $(N \times s) < 1$ , community dynamics are dominated by stochastic process of drift; otherwise they will be influenced by the deterministic process of selection. In general, selection will act to reduce diversity, and will do so more rapidly than drift, resulting in a community comprising the single type with the greatest rate of increase, together with a few rare variants that have appeared in the recent past. This is not necessarily the case, however, if the rate of increase of a type decreases with its frequency in the community. Resource competition may often cause this pattern, because dissimilar types have dissimilar requirements, and rare types will therefore tend to spread because the resources they require are present in relative excess. Diversity is in this case actively maintained through divergent, or balancing, selection. In well-mixed environments (such as the surface waters of a lake) the amount of diversity that is maintained will depend on the relative rates of supply of limiting resources. In viscous environments (such as the soil of a forest) it will depend on the frequency of sites that provide different conditions of growth. The expected amount of diversity cannot be calculated from first principles, because the underlying distribution of different kinds of site in general is unknown.

Deterministic processes are responsible for two fundamental biological processes: the evolution of ecological specialization through natural selection acting on undirected variation, and the development of community structure through the selective sorting of divergently adapted species in a heterogeneous landscape. It does not necessarily follow, however, that the bulk of genetic variation in populations, or the bulk of species diversity in communities, is actively maintained by balancing selection. Granted that adaptation and specialization are often observed, and are always attributable to selection, it remains possible nonetheless that most mutants and most species, in most circumstances, are more strongly affected by stochastic than by deterministic forces.

The clash between neutral and functional (or "selectionist") views of genetic variation was the central issue in population genetics for the generation following the successful application of protein electrophoresis to the problem of measuring variation in the mid-1960s. The unexpectedly large amount of allelic diversity revealed by this technique long resisted an authoritative interpretation despite a vigorous controversy (see Lewontin 1974). Many studies succeeded in showing that fitness components varied in particular sets of electrophoretic variants; but such cases were never decisive because they necessarily embrace only a small fraction of overall variation. Others attempted to compare levels of diversity with those predicted by neutral theory, but they were seldom convincing because the prediction involves a poorly known but large number (effective population size) and an even more poorly known but very small number (mutation rate per locus), whose product will seldom, if ever, be estimated with sufficient accuracy to refute the neutral prediction. A large fraction of the literature is occupied by comparisons of gene frequency distributions with their predicted values. Neutral theory in population genetics, for example, predicts that there will be greater allelic diversity in larger populations; selection theory predicts that distant populations will have similar patterns of allele frequency; and so forth. None of these attempts delivered the knock-out blow, however; despite sophisticated theory and painstaking fieldwork, it was always possible to show that a pattern advanced as support for one theory, might also arise as a consequence of the other. The outcome has been the emergence of "nearly neutral" theory that explicitly considers the interaction of drift and selection on the genome (Ohta 1992, 2002), perhaps the direction in which the current debate within community ecology will move (Chave 2004).

Ironically, this comparable debate about the balance between deterministic and stochastic forces deciding community diversity has only recently begun despite the issue having been raised early on in two classic articles by G. Evelyn Hutchinson (1959, 1961). The theme of unexpectedly high levels of diversity certainly was more clearly apparent to ecologists observing organisms in natural communities than to geneticists working on molecular markers in the laboratory. Perhaps the very ability to observe organisms closely tilted the discussion away from stochastic factors to questions of adaptation and selection. Those more deterministic themes constitute the long tradition of niche studies in community ecology (Schoener 1989). While the neutralist debate raged in population genetics, there were in fact neutral theories, of a sort, being developed in ecology, but not in any connection to work on adaptation and selection. The best known is the theory of island biogeography, which was elaborated with great success by MacArthur and Wilson (1963, 1967), but the implicit equivalence of species within the broad functional categories used by systems ecologists is perhaps equally eloquent (see Duckworth et al. 2000). The few pioneering attempts to explicitly establish a neutral theory parallel to that in population genetics (Caswell 1976, Hubbell 1979) failed to ignite a great debate; the intense discussion of stochastic and deterministic forces that dominated one field found scarcely any echo in the other (Silvertown and Law 1987, Chesson 1991). It is only now, some 50 years after the appearance of Hutchinson's articles, that the issue at the heart of the interpretation of diversity has come into sharp focus in community ecology.

#### The Main Lines of Evidence

#### Abundance

The frequency distribution of abundance among species is the primary determinant of patterns of diversity, because the diversity recorded from a site represents a sample from this distribution. It can take many forms. Fisher et al. (1943) found that more abundant species were less frequent, and by an ingenious statistical argument derived the log-series distribution. Preston (1948) observed that the most frequent category is often made up of species of intermediate abundance, and proposed the log-normal distribution as a descriptive generalization. Subsequent attempts to derive a general theory of species abundance are described briefly by Chave (2004) and at length by Tokeshi (1999). The neutral theory provides a simple mechanistic model of communities that leads to the clear prediction that the form of the distribution of abundance depends on the number of individuals of novel type appearing per generation. It will resemble the geometric or log series when this number is large, and a negatively skewed (long left tail) log-normal when it is small. This has some claim to be the most powerful mechanistic theory in ecology, explaining more than 99% of the variance of abundance among species (McGill 2003; see Volkov et al 2004). In the most extensive compilation of abundance data about 80% of cases resemble negatively skewed lognormal distributions (Halley and Inchausti 2002). It has been derived in two ways. Hubbell (1997, 2001) posited that new types arise by speciation with probability v per birth. The distribution of abundance is then completely specified by  $N \times v$ , and v can be estimated (from the observed distribution) given a good estimate of N. Bell (2000) posited that new types arise by immigration with probability m per species per generation. A more detailed description of the structure of alternative neutral models is given by Chave (2004). Distributions of similar shape can readily be generated by functional theories of abundance. These are less parsimonious, however, insofar as they require additional parameters, such as the underlying distribution of the productivity of niches and the associated set of selection coefficients.

The resemblance of the distribution of abundance to familiar forms such as the log-Normal has led to the suggestion that statistically derived distributions are an alternative to neutral theory (e.g., McGill 2003). This purely empirical approach abandons the attempt to link pattern to process, asserting that a descriptive statistic can be legitimately compared with the outcome of a process governed by a defined mechanism. This position has been defended in previous debates in biology, such as the "empirical ecology" of R. H. Peters (1991), or the biometrical (as opposed to Mendelian) interpretation of morphological variation (see Olby 1989).

# Novelty

Speciation-based neutral models provide a complete and self-consistent account of community dynamics. Their main weakness is that estimates of speciation rates are uncomfortably high. The abundance of birds in Great Britain has been very thoroughly documented (Nee et al. 1991) and yields an estimate of  $v = 3.3 \times 10^{-7}$ (Hubbell 2001:310). This implies that several new species arise in Great Britain every year. Even if most become extinct almost immediately, it seems unlikely that this would have escaped the attention of ornithologists. Since the community as a whole is assumed to be close to equilibrium, as many species should become extinct per unit time as appear. The fraction of all species becoming extinct each year is then roughly 1%, so the average longevity of a species would be about a century. Since molecular phylogenies show that most extant species are more than a million years old (Webb and Gaston 2000), this estimate seems to be about four orders of magnitude in error. Although older (and more abundant) species may be more likely to be recognized, this discrepancy is a serious challenge for speciationbased neutral models (Ricklefs 2003), although it may be resolvable through alternative models of neutral speciation (Hubbell 2003).

Immigration-based models evade the problem of unrealistically high speciation rates, because it is not unreasonable to suppose that a single individual belonging to a type not currently present appears in the community every few hundred generations. Indeed there are many studies that document the interactions between local and regional pools on species diversity in plant communities (Dupré et al. 2002, Pärtel 2002, Ricklefs 2004). The rate of immigration of a given species depends on its frequency in the external pool, whereas this frequency is precisely what the theory is intended to predict. Immigration-based models are not internally self-consistent because of this limitation. At high rates of immigration, this is a serious flaw because the species composition of the target community will be forced by the arbitrarily defined composition of the external pool. If rates are very low, this may not be, in practice, a very severe limitation, and in fact the output of speciation-based and immigration-based models is very similar when the number of individuals of novel type appearing per generation is very small relative to the total number of births.

## Biological surveys

Substantial surveys of species distribution and abundance together with associated measures of environmental variation can be found in the biological and environmental literature going back over a century. These biological surveys adopt diverse methodologies varying in extent, intensity, duration and accuracy (Yoccoz et al. 2001, Tyre et al. 2003). Most involve haphazard or stratified sampling of spatial variation in species distribution and abundance, but some provide systematic grid samples that vary in extent and grain. A systematic biological survey of this sort can yield much additional information on range, diversity, and dispersion (Bell 2001, 2003). These are quantities at the core of ecology and the factors that influence them are the subject of a very large literature. The relationships among them, such as the range-abundance relationship, have also been used extensively to evaluate the importance of different ecological mechanisms (Gaston 2003). In many cases, however, the distribution of quantities such as range follow from the distribution of abundance and the relationships between parameters such as range and abundance obey simple algebraic rules. For example, range (R; the number of sites from which a species has been recorded) and abundance (r; the total number of individuals found in the survey) are related as a power law  $R = a \times r^{z}$ , which can be linearized as  $\log(R) = z[R,r] \times \log(r) + a[R,r]$ . It follows that the range of a species increases with mean local abundance:  $\log(R) = z[R,r/R] \times \log(r/R) + a[R,r/R]$ , where the expected value of the regression coefficient is z[R,r/R] = z[R, r]/(1 - z[R,r]). Both power laws fit the data from plant surveys reasonably well (Bell 2003:Figs. 3A and 4A), but both are readily generated by neutral community models (Bell 2003:Figs. 3B and 4B). Thus, the success of neutral theory in predicting the distribution of abundance implies that it will also be successful in predicting these other attributes of communities, whether at local (Bell 2003) or global (Bell 2001) scales.

Biological surveys may also gather information on the location, the size (or productivity), and the environmental characteristics of sites. These can then be used to identify the ecological correlates of either the bulk diversity or the specific composition of sites. It is usually assumed that these correlations must be attributable to functional differences between species that cause a characteristic set of species to become consistently associated with each different kind of site. It is conceivable, however, that spatial pattern, and covariance with environmental factors, could be created through local dispersal alone in spatially defined neutral models.

# Species-area and diversity-productivity rules

The number of species recorded tends to increase with the extent of the site sampled, and this relationship is very often best described by a power law. The speciesarea rule has been very extensively documented, and the underlying functional mechanisms have been debated at length (reviewed by Rosenzweig 1995). Spatial neutral models generate qualitatively and quantitatively realistic relationships, however, because larger sites support more individuals and thus acquire in each generation more individuals of novel type. Diversity is often strongly correlated with environmental measures that provide indices of biological productivity, at least at large spatial scales (H-Avecedo and Currie 2003) and this can be explained in the same way. The diversityproductivity relationship at various spatial scales and across different ecosystems is less coherent and not as easily attributable to spatial effects (Cornwell and Grubb 2003, Ricklefs 2004).

# Environmental heterogeneity

Correlations of diversity with strong, geographic-scale gradients in climate and habitat variation are well known (Kerr and Packer 1997, Kerr et al. 2001) and persist down to the regional scale (White and Miller 1988, Wohlgemuth 1998, Lobo et al. 2001, Rey Benayas and Scheiner 2002, Deutschewitz et al. 2003, Pausas et al. 2003). Attempts to predict diversity as a function of environmental heterogeneity at more local spatial scales, however, have met with mixed success (Rey Benayas and Scheiner 2002, Bell et al. 2001). Moreover, for the following reasons, spatial neutral models may generate patterns of diversity at any spatial scale that are similar to those anticipated from patterns of environmental heterogeneity. Suppose that the grain of environmental sampling is small relative to the grain of biological sampling, and that the real underlying grain of some patchy environmental factor is about the same as the grain of biological sampling. The survey would then be able to detect an effect of the mean value of this factor on diversity, because biological survey sites are likely to occupy patches with different values of the environmental factor. It is unlikely to be able to detect an effect of the variance of this factor, however, because the environmental samples taken within a biological survey site are likely to represent the same kind of patch. Conversely, if the real grain of the environment is comparable to the grain of the environmental sampling, then the survey is likely to detect any effect of the variance of an environmental factor, because the environment within each biological survey site is heterogeneous and the environmental sampling within this site will supply a good estimate of this heterogeneity. The survey is unlikely to detect any effect of the mean value of the environmental factor, however, because each biological survey site will contain a large proportion of the different kinds of environmental patch The estimate of the mean environment is not biased, but the reduced environmental variance among sites will make it more difficult to detect real differences among sites. The design of the survey thus renders it more likely to detect some effects than others, and this will apply equally to real and to simulated species distributions. If the simulated distributions are projected onto the map of a survey area, a spatial neutral model will thereby generate environmental correlates of bulk diversity, and may even identify the same factors as those found to be correlated with diversity in the biological survey itself.

#### Non-neutral patterns from surveys

Nevertheless, it should not be concluded that neutral models are capable of generating any kind of pattern whatsoever. In particular, they will not give rise to relationships between variables that are modal (hump shaped) or asymmetrical (positively or negatively correlated). The relationship between diversity and productivity is often modal, with maximal diversity at intermediate levels of productivity (Rosenzweig 1995, Cornwell and Grubb 2003). If species are differently adapted, with each having superior performance in some kinds of site but inferior performance in others, then the number of species that can be supported in a region will depend on the number of different kinds of site available, and diversity will be positively correlated with environmental heterogeneity. Patterns such as these cannot be generated by neutral models, and provide strong indirect evidence for functional diversification among species.

#### Degree of specialization

Many species will be recorded from only a fraction of sites, and therefore occupy only a fraction of the range of conditions of growth available to all species within a region. The value of this fraction is an estimate of the precision of local adaptation, with respect to a particular environmental variable: highly specialized species will be confined to sites within a narrow range of values. The frequency distribution of precision can thus be used as an estimate of the mean and variance of the degree of local adaptation within a community. Projecting simulated species distributions onto the map of an area provides estimates of the apparent precision of local adaptation in neutral communities. It was surprising to find that spatial neutral models give rise to frequency distributions of precision that are very similar to those estimated from biological surveys, as a consequence of the spatial patterns produced by local dispersal alone (Bell et al. 2001). Broad patterns such as the relationship between range and specialization are readily generated by neutral models, and should not be uncritically accepted as evidence for functional diversification.

#### Community composition

The specific composition of communities, defined by habit or taxonomy, becomes steadily more different as the distance between them increases. An equivalent way of expressing this pattern is that the combined diversity of two sites increases with the distance between them. This is expected to be the consequence of local adaptation, because environmental variance increases with distance or extent. It may equally arise through local dispersal alone, however, because this necessarily creates positive covariance of species composition between neighboring sites. In neutral models, the rate of turnover, and thereby the partition of diversity, is simply a function of the rate of local dispersal. The contributions of selection and dispersal cannot usually be separated in survey data, because both are related to the distance between sites. A statistical partitioning of environment from distance (Borcard et al. 1992) may be informative, but is not necessarily decisive. First, the patchy distribution of species in a neutral community will produce fortuitous correlations with environmental factors, and removing this covariance will necessarily decrease the quantity of variance attributable to distance alone. Secondly, using a permissive criterion (such as P< 0.25) to remove potential covariates from an extensive list of candidate factors will readily generate regression models with high explanatory power and very low fiducial probability, even from random data (Freedman 1983). The behavior of neutral models in this regard has not yet been studied, but it seems likely that the approach through environmental correlation will be decisive only if the factors held to be responsible for variation in community composition are specified in advance of the analysis, from physiological principles, or on the basis of prior knowledge from other regions.

## Codistribution

The approach through environmental correlation risks failing to identify the most important environmental factors, so that negative results are indecisive. An alternative approach is to use the species distributions themselves to calculate the correlations between pairs of species over sites. If species are locally well adapted, then species with similar specializations will usually be found together, whereas those with different specializations will usually be found apart, creating a broad range from large positive to large negative correlations. This is an attractive procedure because it necessarily gives the proper weight to all environmental factors. In the past, ecologists have compared observed patterns of codistribution with those arising from random species distributions (see Gotelli and Graves 1996). Neutral models will usually give rise to strikingly nonrandom patterns of codistribution, with many more extreme correlations than expected. It is difficult to distinguish these from the outcome of local adaptation, unless selection is very strong (G. Bell 2005).

## Divergence of community composition

The variance of independent (completely isolated) neutral communities increases linearly through time, leading to marked geographical variation in community composition. The variance of abundance of genera of trees among localities in southern Ontario, estimated from pollen in lake sediments, does not show a consistent tendency to increase through time, which seems inconsistent with neutrality (Clark and McLachlan 2003). The flaw in this argument is that it applies only to completely isolated communities, and does not necessarily hold when there is any appreciable rate of local dispersal (Volkov et al. 2004), given that regional extinction is prevented by immigration from an external pool of fixed species composition. Even though sampling sites are spread over a large area, local dispersal between neighboring sites will create correlation between distant sites despite the lack of direct long-distance dispersal. If a single individual of novel type appears in each local community per generation by local dispersal, community composition will be largely homogenized over the entire sampling area, however large.

## Dynamic insufficiency of current theory

There is very extensive experimental evidence confirming that the necessary conditions required by the functional interpretation are generally satisfied. Plots that are given different treatments will often develop distinctively different plant communities (Dodd et al. 1994) assembled through competition (Fargione et al. 2003). Adaptive radiation can be observed in microcosm experiments (MacLean and Bell 2002), where diversity can be maintained through negative frequency-dependent selection (Rainey and Travisano 1998) and is modulated by productivity (Kassen et al. 2000) and disturbance (Buckling et al. 2000). Mixtures of species often yield more than the average of their components in the laboratory (Bell 1990) and in the field (Hector et al. 1999). Finally, largescale reciprocal transplant experiments have provided direct evidence of local adaptation (Belotte et al. 2003). It might be expected, then, that the very detailed and extensive data on distribution and abundance available from biological surveys would provide decisive documentation of local adaptation, confirming the functional theory. Nothing of the kind has happened. Instead, almost all the major patterns emerging from surveys can be interpreted equally well by a simpler theory. Why has comparative analysis failed to discriminate between two theories that, on the face of it, supply completely contrary interpretations of communities?

The explanation, we believe, is that current theory is incapable of providing predictions that can be tested readily with realistic survey data. To illustrate this point, imagine a landscape consisting of many different kinds of equally productive site, arranged at random. A single species is well adapted to any particular kind of site, where all others are at a disadvantage, expressed by the selection coefficient s. With s = 0, the model is neutral, and for an arbitrary but reasonable set of demographic parameters gives rise to two familiar results: the distribution of abundance, resembling a left-skewed log-normal, and the decay of similarity, which declines asymptotically towards zero with increasing distance between sites. With strong selection (s = 0.5) each site is occupied almost exclusively by the locally adapted type; thus, all species have nearly equal abundance, and similarity decreases very rapidly, approaching zero at distances exceeding the dispersal achieved in a single generation. There is, then, a marked difference between neutral and functional models. Selection may not be universally strong, however. It may be generally weak (s =0.05); or it may be strong but exceptional, such that all species at any given site are well adapted, except one. In either case, both the distribution of abundance and the decay of similarity with distance are effectively indistinguishable from a neutral model (Fig. 1). The main patterns, both spatial and nonspatial, that emerge from surveys may be dominated by stochastic neutral processes, even when well-defined selective processes are operating in the community. Chave et al. (2002) reached a similar conclusion.

# Spatial and phylogenetic considerations in analysis of survey data

There are, however, two ways in which the functional signal concealed in survey data might be amplified so as to refute a neutral interpretation. To illustrate them we shall refer to detailed surveys of sedges (Cyperaceae: *Carex*) and other vascular plants in a 1000-ha fragment of old-growth forest in the Gault Nature Reserve at Mont St-Hilaire, Quebec ( $45^{\circ}31'$  N,  $73^{\circ}08'$  W) that is little disturbed by human activity and has high levels of plant diversity. The sedges in the genus *Carex* are a species-rich group of ecologically similar species, with the 55 species occurring in the reserve providing an especially interesting and challenging natural system for

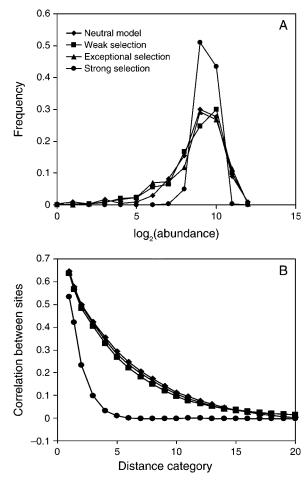


FIG. 1. The effect of the intensity of selection (*s*) on (A) the distribution of abundance and (B) the decay of community similarity with distance. A community of 80 species inhabits a grid of 1600 sites, each of which supports a maximum of 50 individuals. There are 80 different kinds of sites, each determined by a random draw from a uniform distribution, arranged at random. Each individual has birth rate b = 0.8(1 - s), death rate d = 0.5, and probability of dispersal as a newborn to a neighboring site of u = 0.1. The four models are (a) neutral (s = 0); (b) weak selection, all species except one poorly adapted to each kind of site (s = 0.5); (c) exceptional selection, all species except one poorly adapted to each kind of site (s = 0.5); (d) strong selection, all species except one poorly adapted to each kind of site (s = 0.5).

testing ideas about the nature of community diversity (Lechowicz and Bell 1991, Bell et al. 2000, 2001).

The first approach is to dissociate environmental variance from distance in spatially defined data, so that the decay of similarity attributable to distance alone can be estimated. By taking advantage of the defined spatial structure in a survey, it is possible to statistically dissociate environmental variance from distance in spatially defined data, so that the decay of similarity attributable to distance alone can be estimated as a test of neutral predictions. A problem with this approach is that in many, perhaps most, environments, space and distance cannot be dissociated in a simple analysis of

TABLE 1. Phylogenetically based comparative analysis of the distribution of *Carex* spp. at Mont St-Hilaire in relation to a range of environmental factors.

Environmental factor	Mean	$MS_W$	$MS_{S\subset C}$	MSC	VR(species)	VR(clades)
Elevation	231	6247	94326	95118	15.1	1.01
Insolation	503	1637	10585	2141	6.47	<1
ln(flow/slope)	6.90	0.486	5.239	7.182	10.8	1.37
pH	5.51	0.385	1.144	1.090	2.14	<1

*Notes:* For each factor,  $MS_W$  is the mean square within species,  $MS_{S\subset C}$  is the mean square for species within clades, and  $MS_C$  the mean square for clades. The clades used are: (1) *C. communis* + *C. pensylvanica* + *C. peckii* + *C. rugosperma*; (2) *C. laxiflora* + *C. albursina* + *C. blanda* + *C. ormostachya* + *C. leptonervia*; (3) *C. arctata* + *C. gracillima* + *C. hirtifolia*; (4) *C. deweyana* + *C. bromoides*; (5) *C. rosea* + *C. applachica* + *C. radiata*; (6) *C. platyphylla* + *C. plantaginea*; (7) *C. intumescens* + *C. houghtoniana* + *C. hystericina* + *C. lupulina* + *C. comosa*. Species distributions were mapped at a grain of 1 ha. Elevation, insolation, slope, and flow were estimated from a digital elevation model of the mountain for all 25<sup>m<sup>2</sup></sup> pixels. Flow/slope is an index of soil wetness. Soil pH was measured from samples taken from each hectare by the method described by Bell et al. (2001). The variance ratio (VR) for species within clades is *F* with df = 6, 4828 and is significant (*P* < 0.0001) in all cases. The *P* = 0.05 point for clade is  $F_{6,17} = 3.28$ .

variance-there is a troublesome distance-by-environment covariance on natural landscapes. An alternative approach is to choose a subset of sites, at each of which a wide range of environmental factors has been estimated or measured, in such a way that there is no consistent tendency for environmental variance to increase with distance (Gilbert and Lechowicz 2004). Any remaining decay of community similarity with distance must then be attributed to neutral processes (or to species interactions involving unidentified environmental factors affecting growth). This has been done for sample plots at Mont St-Hilaire and has yielded convincing evidence for the dominance of environmental factors in determining species distribution and abundance in diverse phylogenetic and functional groups of vascular plants in the forest understory, including species of Carex (Gilbert and Lechowicz 2004). These investigations involved direct measurements of many environmental variables and were done at finer spatial scales (10- and 50-m<sup>2</sup> nested quadrats) than our previous grid surveys, which also may have contributed to the strength of the environmental signal detected.

A second possibility is that a phylogenetic comparative analysis might readily falsify the neutral interpretation. The phylogeny of a neutral community (if it possesses one) is uninformative, because no ecological attributes are associated with species membership. If related species are found to be ecologically similar, therefore, there must be a consistent functional diversification of clades. We emphasize that variance within clades is not necessarily informative: species will differ in their ecological covariates, because distributions are patchy. If there is no variation among clades, then all the among-species variance will appear as within-clade variance. It is consistent among-clade variance that is unarguably non-neutral. To illustrate this procedure, we have used the detailed environmental information available at Mont St-Hilaire, in conjunction with a robust molecular phylogeny for the resident sedges (Waterway and Starr, in press; M. J. Waterway, unpublished data). We chose distinct monophyletic clades, each of which had one common species and at least one other species recorded from the survey, giving a total of 24 species in seven clades. A two-level nested analysis of variance was then used to partition the variance among species within clades from the variance among clades. It is the variance among clades that constitutes evidence for non-neutral distributions. The data for several physical environmental factors thought to affect plant distribution shows that there is in every case significant variance among species within clades (Table 1). By contrast, the mean square among clades does not consistently exceed the mean square among species within clades. The highly unbalanced nature of the data set (common species are two orders of magnitude more frequent than rare species) deters us from assigning formal significance to this result, but, in any case, all variance ratios fall well below the P = 0.05level for balanced data. This result is thus suggestive, but indecisive. We are nonetheless enthusiastic about the broader application of phylogenetics to survey data. More precise phylogenetic information will enable us to date nodes, and thus evaluate the extent of divergence within and among clades. More precise environmental information, obtained through plant-based sampling, will enable us to identify the range of conditions occupied by each species, without the uncertainty associated with relatively coarse-grained grid surveys. Phylogenetic analyses are likely to be simpler and more powerful than spatial analyses, because no confounding source of variance need be removed. We suggest that phylogenetically based analysis may be the most effective tool that can make use of survey data to reveal functional diversification within communities.

In conclusion, we argue that community properties are often strongly influenced by stochastic processes of drift, which are likely to obscure deterministic processes of selection, unless there are strong functional differences among most species at most sites. For this reason, neutral theory will generate a good first approximation to the most prominent patterns that form the subject matter of community ecology and macroecology, even in the presence of consistent processes of selection, such as would be detected by the appropriate manipulation of environments or communities. The non-neutral signal in survey data can be detected unambiguously only by the careful partitioning of environmental or phylogenetic effects, and determining the relative contribution of neutral and functional processes to community patterns has only just begun.

#### Acknowledgments

This research was supported principally by Le Fonds Québécois de la Recherche sur la Nature et les Technologies. We thank the dedicated students who conducted the *Carex* survey in the Gault Nature Reserve and McGill University for its commitment to preservation of this old-growth forest.

#### LITERATURE CITED

- Bell, G. 1990. The ecology and genetics of fitness in *Chlamydomonas*. II. The properties of mixtures of strains. Proceedings of the Royal Society of London, Series B, Biological Sciences **240**:323–350.
- Bell, G. 2000. The distribution of abundance in neutral communities. American Naturalist 155:606–617.
- Bell, G. 2001. Neutral macroecology. Science 293:2413-2418.
- Bell, G. 2003. The interpretation of biological surveys. Proceedings of the Royal Society of London, Series B, Biological Sciences 270:2531–2542.
- Bell, G. 2005. The co-distribution of species in relation to the neutral theory of community ecology. Ecology 86:757–770.
- Bell, G., M. J. Lechowicz, and M. J. Waterway. 2000. Environmental heterogeneity and species diversity of forest sedges. Journal of Ecology 88:67–87.
- Bell, G., M. J. Lechowicz, and M. J. Waterway. 2001. The precision of adaptation in forest plants. Pages 117–138 *in* J. Silvertown and J. Antonovics, editors. Integrating ecology and evolution in a spatial context. 14th Special Symposium of the British Ecological Society. Blackwell Science, Oxford, UK.
- Belotte, D., J. B. Curien, R. C. Maclean, and G. Bell. 2003. An experimental test of local adaptation in soil bacteria. Evolution **57**:27–36.
- Borcard, D, L. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73: 1045–1055.
- Buckling, A., R. Kassen, G. Bell, and P. Rainey. 2000. Disturbance and diversity in experimental microcosms. Nature 408:961–964.
- Caswell, H. 1976. Community structure: neutral model analysis. Ecological Monographs **46**:327–354.
- Chave, J. 2004. Neutral theory and community ecology. Ecology Letters 7:241–253.
- Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. American Naturalist 159:1–23.
- Chesson, P. 1991. A need for niches? Trends in Ecology and Evolution 6:26–28.
- Clark, J. S., and J. S. McLachlan. 2003. Stability of forest biodiversity. Nature **423**:635–638.
- Cornwell, W. K., and P. J. Grubb. 2003. Regional and local patterns in plant species richness with respect to resource availability. Oikos 100:417–428.
- Deutschewitz, K., A. Lausch, I. Kuhn, and S. Klotz. 2003. Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. Global Ecology and Biogeography 12:299–311.
- Dodd, M. E., J. Silvertown, K. McConway, J. Potts, and M. Crawley. 1994. Stability in the plant communities of the Park Grass Experiment: the relationships between species richness, soil pH and biomass variability. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 346:185–193.
- Duckworth, J. C., M. Kent, and P. M. Ramsay. 2000. Plant functional types: an alternative to taxonomic plant community description in biogeography. Progress in Physical Geography 24:515–542.

- Dupré, C., C. Wessberg, and M. Diekmann. 2002. Species richness in deciduous forests: effects of species pools and environmental variables. Journal of Vegetation Science 13: 505–516.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences (USA) 100:8916–8920.
- Fay, J. C., and C.-I. Wu. 2001. The neutral theory in the genomic era. Current Opinion in Genetics and Development **11**:642–646.
- Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample from an animal population. Journal of Animal Ecology 12:42–58.
- Freedman, D. A. 1983. A note on screening regression equations. American Statistician 37:155–158.
- Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press, Oxford, UK.
- Gilbert, B., and M. J. Lechowicz. 2004. Neutrality, niches, and dispersal in a temperate forest understory. Proceedings of the National Academy of Sciences (USA) 101:7651–7656.
- Gotelli, N. J., and G. R. Graves. 1996. Null models in ecology. Smithsonian Institution Press, Washington, D.C., USA.
- H-Acevedo, D., and D. J. Currie. 2003. Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment. Global Ecology and Biogeography **12**:461–473.
- Halley, J., and P. Inchausti. 2002. Lognormality in ecological time series. Oikos **99**:518–530.
- Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127.
- Hubbell, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. Science **203**:1299–1309.
- Hubbell, S. P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. Coral Reefs **16**:S9–S21.
- Hubbell, S. P. 2001. A unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Hubbell, S. P. 2003. Modes of speciation and the lifespans of species under neutrality: a response to the comment of Robert E. Ricklefs. Oikos 100:193–199.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals. American Naturalist 93:145–159.
- Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist **95**:137–145.
- Kassen, R., A. Buckling, G. Bell, and P. Rainey. 2000. Diversity peaks at intermediate productivity in a laboratory microcosm. Nature 406:508–512.
- Kerr, J. T., and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature 385:252–254.
- Kerr, J. T., T. R. E. Southwood, and J. Cihlar. 2001. Remotely sensed habitat diversity predicts butterfly species richness and community similarity in Canada. Proceedings of the National Academy of Sciences (USA) 98:11365–11370.
- Kimura, M. 1983. The neutral theory of molecular evolution. Cambridge University Press, Cambridge, UK.
- Lechowicz, M. J., and G. Bell. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. Journal of Ecology **79**:687–696.
- Lewontin, R. C. 1974. The genetic basis of evolutionary change. Columbia University Press, New York, New York, USA.
- Lobo, J. M., I. Castro, and J. C. Moreno. 2001. Spatial and environmental determinants of vascular plant species richness distribution in the Iberian Peninsula and Balearic Islands. Biological Journal of the Linnaean Society 73:233–253.
- MacArthur, R. H., and E. O. Wilson. 1963. Equilibrium theory of insular zoogeography. Evolution 17:373–395.

- MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Monographs in population biology. Princeton University Press, Princeton, New Jersey, USA.
- MacLean, R. C., and G. Bell. 2002. Experimental adaptive radiation in *Pseudomonas*. American Naturalist 160:569–581.
- McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. Nature 422:881–885.
- Nee, S., P. H. Harvey, and R. M. May. 1991. Lifting the veil on abundance patterns. Proceedings of the Royal Society of London, Series B, Biological Sciences 243:161–163.
- Ohta, T. 1992. The nearly neutral theory of molecular evolution. Annual Review of Ecology and Systematics 23: 263–286.
- Ohta, T. 2002. Near-neutrality in evolution of genes and gene regulation. Proceedings of the National Academy of Sciences (USA) 99:16134–16137.
- Olby, R. 1989. The dimensions of scientific controversy: the biometric-Mendelian debate. British Journal of the History of Science **22**:299–320.
- Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale. Ecology 83:2361–2366.
- Pausas, J. G, J. Carreras, A. Ferre, and X. Font. 2003. Coarsescale plant species richness in relation to environmental heterogeneity. Journal of Vegetation Science 14(5):661–668.
- Peters, R. H. 1991. A critique for ecology. Cambridge University Press, Cambridge, UK.
- Preston, F. W. 1948. The commonness and rarity of species. Ecology 29:254–283.
- Rainey, P. B., and M. Travisano. 1998. Adaptive radiation in a heterogeneous environment. Nature 394:69–72.
- Rey Benayas, J. M., and S. M. Scheiner. 2002. Plant diversity, biogeography and environment in Iberia: patterns and possible causal factors. Journal of Vegetation Science 13: 245–258.
- Ricklefs, R. E. 2003. A comment on Hubbell's zero-sum ecological drift model. Oikos 100:185–192.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. Ecology Letters 7:1–15.

- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Schoener, T. W. 1989. The ecological niche. Pages 79–114 in J. M. Cherrett, editor. Ecological concepts: the contribution of ecology to understanding of the natural world. Blackwell Scientific, Oxford, UK.
- Silvertown, J., and R. Law. 1987. Do plants need niches? Some recent developments in plant community ecology. Trends in Ecology and Evolution **2**:24–26.
- Tokeshi, M. 1999. Species coexistence: ecological and evolutionary perspectives. Blackwell Science, Oxford, UK.
- Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris, and H. P. Possingham. 2003. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. Ecological Applications 13:1790–1801.
- Volkov, I., J. R. Banavar, A. Maritan, and S. P. Hubbell. 2004. The stability of forest diversity. Nature 427:696–697.
- Waterway, M. J., and J. R. Starr. *In press*. Phylogenetic relationships in tribe Cariceae (Cyperaceae) based on nested analyses of four molecular data sets. In J. T. Columbus, E. A. Friar, C. W. Hamilton, J. M. Porter, L. M. Prince, and M. G. Simpson, editors. Monocots: comparative biology and evolution. Rancho Santa Ana Botanic Garden, Claremont, California, USA.
- Webb, T. J., and K. J. Gaston. 2000. Geographic range size and evolutionary age in birds Proceedings of the Royal Society of London, Series B, Biological Science 267(1455): 1843–1850.
- White, P. S., and R. I. Miller. 1988. Topographic models of vascular plant richness in the southern Appalachian high peaks. Journal of Ecology **76**:192–199.
- Wohlgemuth, T. 1998. Modelling floristic species richness on a regional scale: a case study in Switzerland. Biodiversity and Conservation **7**(2):159–177.
- Yoccoz, N. G., J. D. Nichols, and T. Boulinier. 2001. Monitoring of biological diversity in space and time. Trends in Ecology and Evolution 16:446–453.