

## Challenges to understanding dynamics of biodiversity in time and space

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The negative consequences of anthropogenic activities such as agriculture and urbanization (e.g., deforestation, greenhouse gas emissions, and pollution) have become exacerbated by rapid rates of human population increase (see Pimm et al. 2001). Subsequent habitat loss and modification has accelerated rates of extinction, creating a biodiversity crises which arguably is one of the most pressing problems of the twenty-first century. Although causative agents are unclear, the fossil record suggests that biotas undergo periods of massive extinction as well as considerable diversification (Alroy et al. 2001; Jackson and Johnson 2001) at the global scale, even in the absence of human activities. As such, quantifying the spatial and temporal dynamics of biodiversity in past and contemporary times, and understanding their mechanistic bases represent disciplinary emphases of evolutionary and environmental biology. Equally important, such understanding is a critical step in informing regional as well as global management strategies and conservation efforts. Nonetheless, considerable controversy or uncertainty exists surrounding the patterns, underlying mechanisms, and strategies of conservation (Willig 2000; Andelman and Willig 2002). The past may provide important insights into a number of relevant issues regarding contemporary biodiversity (and vice versa), but only recently has the dialogue between neontologists and paleontologists charted productive areas of collaboration. Indeed, a growing body of work has questioned the meaning of global measures of biodiversity (past or present) and has suggested that only detailed studies at local sites provide resolution to important issues about biodiversity. This is due, in part, to considerable sampling

problems associated with broad-scale estimation, including the averaging of local and regional patterns.

In my view, significant progress has occurred in understanding the dynamics of biodiversity in time and space (e.g., see Brown 1995; Rosenzweig 1995), even though a number of thorny issues and challenges limit synthetic or comprehensive understanding. In particular, I address four factors that limit current understanding of biodiversity. These include (1) failure to consider the multidimensional nature of biodiversity, (2) the biases of estimation from constrained sampling, (3) the inherent scale-dependence of biodiversity, and (4) an incomplete understanding of the connection between local and regional processes and patterns.

### Multidimensional Characteristics of Biodiversity

Biodiversity has been characterized as the variation of life on Earth (Wilson 1988). Taxonomic, functional, phenotypic, and genetic attributes imbue the concept with an inherent multidimensional meaning (Solbrig 1991). Nonetheless, few broad scale-scale studies have quantified spatial variation in any aspects of taxonomic diversity other than taxonomic richness (usually at the specific or generic level). Considerably less is known about spatial variation in genetic, phenotypic, and functional components of biodiversity, or their cross-correlations. Recent research (Stevens and Willig 2002) focusing on the full complement of taxonomic diversity at the species level (i.e., diversity, richness, evenness, and dominance) has shown that spatial variation in bat species richness is independent of spatial variation in species evenness across a broad eco-

logical spectrum of local sites ranging from 42°N to 24°S latitude in the New World. Thus, measuring a single component of taxonomic diversity (i.e., species richness) in time or space may not necessarily reveal salient variation in other components of taxonomic diversity, much less dimensions of biodiversity related to function, phenotype, or genetics. Moreover, that same research explored the connection between species richness at the site level and richness at the level of regional species pools. Importantly, the rate of increase in richness with latitude was much steeper for regional pools than for local sites. Variation in richness increased toward the Tropics as well. Consequently, the degree to which alpha diversity (often estimated as the taxonomic richness of a local site) is a surrogate for gamma diversity (considered to be the comparable taxonomic richness of a larger region in which such local sites occur), and vice versa, has a spatial component, with beta diversity (turnover in taxonomic identities among sites within a region) increasing toward tropical areas. In a different context, it has been shown that the design of a system of conservation reserves based on regional estimates of diversity versus local estimates of diversity for the biota of country such as Paraguay (Willig et al. 2000) can be quite different (Andelman and Willig 2002). Clearly, a single metric or surrogate may not capture the essence of biodiversity, and may not adequately reflect variation in space or time.

### **The Challenge of Estimation**

An appropriate sampling protocol is necessary to assess dynamics of biodiversity in time and space accurately. Unfortunately, most macroecological or paleontological studies are not amenable to the same rigors of experimental design and manipulation that characterize other fields of science because of issues related to practicality, feasibility, or ethics. Fortunately, simulation approaches (e.g., bootstrapping and rarefaction) offer much promise for use in estimating various components of biodiversity or in comparing estimates of biodiversity when sampling efforts are not standardized. A growing body of work (e.g., see Gotelli and Graves 1996; and

references therein) suggests a variety of powerful tools for use in overcoming the limitations imposed by sampling constraints. Taphonomic or behavioral differences among species can result in samples being a nonrandom representation of the assemblages from which they are taken. The extent to which collections of extant or fossil specimens are subject to this difficulty compromises accurate estimation of all parameters of biodiversity. Nonetheless, simulation techniques that incorporate various degrees of bias in recovery or detection of individuals or species should be explored as a way to understand the magnitude of the problem.

Of all the components of taxonomic diversity, those primarily reflective of the number of species in an area (e.g., species richness) may be most sensitive to sampling limitations. In contrast, components that include considerations of the relative abundance of species (e.g., species diversity or dominance) may be much less sensitive to the addition of species from the right-hand tail of the rank-abundance distribution for an area. Using resampling procedures, Stevens and Willig (2002) have shown that spatial patterns associated with latitude were insensitive to appreciable reductions in sampling effort for most of the 14 measured metrics of taxonomic diversity. Thus, even if the absolute metrics may be inaccurate, the detection of patterns was reasonably robust to even 75% reductions in effort. To the extent that this phenomenon is true for a variety of taxa in other places or times, there is reason for optimism.

### **Scale Dependence**

Perhaps the three most widely studied phenomena in neontology concerning biodiversity relate to the way in which species richness changes with area (or sampling effort), latitude, or productivity. In fact, the three are inextricably connected to understanding spatial dynamics of biodiversity. Indeed, the growing consensus is that many spatial patterns of biodiversity should be scale-dependent (Scheiner et al. 2000), because the parameters of the power function (representing the way in which richness increases with area) likely are affected by environmental gradients (see Pas-

tor et al. 1996 and Waide et al. 1999 for productivity and Lyons and Willig 1999, 2002 for latitude). Moreover, the mechanisms promoting or limiting biodiversity at one focal scale may be quite different than the analogous mechanisms operating at a different focal scale (e.g., ecological factors at local scales and historical or evolutionary factors at global scales). Thus, samples that integrate different or unknown spatial extents, and by analogy different or unknown temporal extents, should be used with extreme caution.

### Beta Diversity and Body Size

Many recent studies of biodiversity have emphasized the importance of spatial heterogeneity and beta diversity in affecting gamma diversity (Loreau 2000; Chase and Leibold 2002). The translation of heterogeneity among sites into the cumulative gamma diversity of a large region in part depends on the perception of the organisms (e.g., fine grained versus coarse grained sensu Levins 1968 and Kolasa and Pickett 1991). Consequently, as a clade diversifies over evolutionary time, the mean perception of the species in the clade may be changing, especially if mean body size is changing. As a result, relationships between gamma diversity of a clade and time may arise because of body size evolution.

### Synopsis

Considerable progress has been made in documenting spatial and temporal patterns of biodiversity. Deeper understanding involves the identification of causal mechanisms, as well as the realization that data limitations and biases may affect results. The challenge is to assess the sensitivity of conclusions to possible data limitations and biases, and to evaluate questions from multiple scales. Although the distinction between paleontology and neontology may be practical, it is not necessarily natural or productive. Efforts of syntheses that are directed toward biodiversity would benefit from full consideration of knowledge concerning the dynamics of past and present biotas, as well as from incorporating the perspectives and methodologies that are used in both disciplines. Forecasting the future with accuracy requires substantial

reliance on understanding the present and past, and the mechanisms that link them.

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