


BIODIVERSITY *Dynamics*

TURNOVER OF
POPULATIONS, TAXA,
AND COMMUNITIES

Michael L. McKinney
and James A. Drake, *Editors*

Biodiversity Dynamics
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Editors

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Biodiversity Dynamics

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*This book is dedicated to Michael L. Rosenzweig and James H. Brown
for their decades of work to promote interdisciplinary discoveries
between ecology and paleontology.*

– Introduction

Michael L. McKinney

Ecologists must take a more active role in investigating the processes of species production and extinction.

—RICKLEFS AND SCHLUTER 1993B

The biodiversity crisis has had at least one positive outcome: It has forced biologists from many disciplines to interact and exchange data, which generally improves our overall understanding of ecology and evolution. *Biodiversity dynamics* refers to the turnover of biological units across all temporal and spatial scales (chapter 1). Like most of the recent literature on biodiversity, this book represents a synthesis and distillation of data derived from a variety of disparate fields that have traditionally had little interaction. In this case, data from population biology are presented with data from community ecology, comparative biology, and paleontology. Major theoretical and practical gains can be made from such a synthetic view.

This book has its roots in a symposium jointly sponsored by the Ecological Society of America and the American Institute of Biological Sciences, at their 1994 national meeting. Many of the book contributors gave papers at that symposium. However, as the scope and goal of the book became clearer, other contributors were invited to submit papers to help satisfy gaps or deficiencies. In many ways, this book can be seen as an extension of the recent books by James Brown (1995) and Michael Rosenzweig (1995), which seek to extrapolate ecological dynamics to large scales of time and space.

Theoretical Importance of Turnover Across Many Scales

The need for a broad view of biodiversity dynamics has often been expressed by both ecologists (e.g., Pimm 1991) and paleontologists (e.g., Morris 1995a). Ecologists have tended toward an ahistorical focus on general principles of current biotic interactions at relatively small scales of time and space. Paleontologists (and evolutionary biologists in general) have tended toward the other extreme, taking a historical view of biotic interactions at very coarse scales of time and space. Also, ecologists have often emphasized generality dynamics, whereas evolutionists have tended to emphasize the lack of generality found in contingent “random” events (e.g., Gould 1989a).

This book seeks a middle ground, to relate processes occurring at fine and coarse scales while acknowledging that both general dynamics and contingent events are important. To understand the processes controlling diversity at any scale, one must examine both origination and extinction (see also McGhee 1996). Furthermore, we should ideally try to interrelate origination and extinction across many scales. Unlike the theories of some (e.g., Gould 1985), the theme of this book does not emphasize the independence of turnover across various scales of space and time, which would hold, for example, that mass extinctions select victims in ways unrelated to “normal” background extinctions.

To the contrary, much of this book provides evidence that there is often a direct correlation of turnover dynamics across many scales. It is important to realize that much of this evidence is empirical because, in theory, there are many ways that independence among scales could occur. Metapopulation theory, for instance, predicts that a species composed of many small local populations that undergo frequent extinction and recolonization could persist longer than a species composed of just one or a few long-lasting populations (Hanski and Gilpin 1997). In this case, high population extinction rate does not correlate with high species extinction rate. Yet Susan Harrison’s chapter, discussed later, reviews empirical data that suggest this is not so. Real taxa do not persist as classic metapopulations but show dynamics that often link increasing population persistence to increasing species persistence. Similar evidence for extrapolated turnover patterns is also found when examining communities. Chapters by Russell and Aronson and Plotnick show how many patterns of turnover are extrapolated from local communities to the biosphere.

Practical Application of Turnover to Biodiversity Issues

The study of turnover has taken on a new urgency with the rise of conservation biology. We need to examine how human impacts at small scales trans-

late into biodiversity loss at coarser temporal and spatial scales (Meffe and Carroll 1994). Many papers in this volume provide practical information that can be of immediate use to management of biodiversity at many scales.

At the fine scale of population dynamics, Maurer and Nott show evidence from birds detailing why rare species are especially prone to extinction: They have not only smaller ranges but also more fragmented ranges. Conservation management must therefore specifically focus on counteracting the effects of enhanced range fragmentation in rare species.

Data discussed by Cutler, at the coarser scale of community turnover over thousands of years, show a surprising determinism in extinction selectivity among component species. Populations of the same species seem most prone to extinction at many spatial and temporal scales.

At still coarser scales of species turnover in evolutionary time, Gittleman and others, for example, use phylogenetic reconstruction to show that carnivores have tended to experience relatively high extinction rates in the recent past, indicating that they are currently exceptionally vulnerable to extinction. This can help justify placing very high priority on immediate efforts toward their preservation.

At even coarser scales, such as North American mammalian biodiversity in evolutionary time, Alroy reviews considerable evidence that evolutionary diversification will slow down as niche saturation sets limits on the number of species that can be sustained in a region. This has very important implications for making large-scale predictions of biodiversity conservation. For example, long-term regional impacts of introduced species and habitat loss can be based on species–area considerations to predict the final equilibrium diversity that a region can sustain.

Overview of the Book

In the first chapter of this book, I present a broad overview of what is meant by *biodiversity dynamics*. My basic view is that it represents turnover across all scales of time and space. How, for example, is turnover (colonization/extinction) of populations related to turnover (speciation/extinction) of species and higher taxa? The focus is on turnover because it is the only way to gain a full understanding of ecological and evolutionary processes. Information that is limited to either extinction or speciation alone can be very misleading. For one thing, extinction and speciation (and colonization) are often strongly interdependent. Mass extinction may precede major speciation events by removing incumbent species, for example. Or the same physical environmental change may stimulate both speciation and extinction. Even aside from extrinsic causation, there is an intrinsic (biotic) correlation, in

that groups with high speciation rates also tend to have high extinction rates (e.g., Stanley 1990c).

Part One: Phylogenetic Turnover: From Populations Through Higher Taxa

The relation of population turnover to species turnover is most directly addressed by Susan Harrison. Her work has often reviewed empirical data showing that some of the basic assumptions of metapopulation theory do not apply to real species (e.g., Harrison 1994). In her chapter, she thus argues that taxa are not likely to persist in evolutionary time as metapopulations in the classic sense. She discusses how species, instead of persisting as populations in an extinction–colonization equilibrium, tend to show mainland–island, nonequilibrium, or very patchy distributions that show much less or much more colonization among patches than in the restrictive assumptions of metapopulation theory (see also Harrison and Hastings 1996). In the case of mainland–island and nonequilibrium distributions, the persistence of the species is often strongly correlated with the persistence of single (large) populations.

The relationship between geographic range and evolution is examined by Brian Maurer and Philip Nott. They show, using data from North American insectivorous birds, that rare species, with small geographic ranges, also tend to have more fragmented ranges. This synergism between localization and fragmentation means that rare species have relatively higher extinction rates and lower net diversification rates than abundant species. This is supported by fossil data demonstrating that globigerinids had consistently higher net species diversity with lower extinction and speciation than globorotaliids. They discuss how the origin of this pattern may lie in Darwin's idea that more ecologically generalized species, such as the globigerinids, are more locally abundant and widespread (also see Brown 1995). Such species have lower speciation and extinction rates than rare species, with diversification rate (which equals speciation rate minus extinction rate) being greater in more generalized (more common) species.

The next two chapters address turnover at the species level, using the fast-growing methods of phylogeny reconstruction based on living species. John Gittleman and coauthors present a very stimulating overview that covers a wide range of key issues. They show that molecular phylogenies have major practical applications too. A basic theme of their paper is that ecological, life history, and morphological traits are not free to evolve as needed but are phylogenetically constrained to varying degrees (also see Harvey 1996 for review). Using a large database of mammalian molecular phylogenies, they

show that morphological and life history traits are generally less evolutionarily labile than behavioral and ecological traits such as population density and day range. This implies that the latter traits are less constrained by developmental, genetic, or other correlated limitations.

Jody Hey and coauthors test specific models of speciation and extinction with phylogenetic trees of living taxa. This approach expands on the basic random cladogenetic models produced by David Raup beginning in the early 1970s. A key finding is that 10 of the 11 data sets analyzed are best fit by a growth model with an extinction rate of zero. This constitutes tentative evidence that these small young clades are in a growth phase of cladogenesis, although this is not conclusive because of the difficulty in distinguishing extinction from sampling bias and other artifacts.

In the past few years, Daniel McShea has written some very influential articles on evolutionary trends, especially the evolution of complexity (McShea 1996). In his chapter, he extends earlier work to develop a conceptual scheme on clade diversification in state space (where *state space* is any feature of a species such as size, geographic range, or complexity). He shows that large-scale behavior of a clade, such as a trend in the mean or maximum of a trait, is the product of two factors: (1) the clade's small-scale behavior, i.e., rules governing the individual lineages of the clade, and (2) the structuring of those rules in state space. If structuring is minimal, then large-scale clade patterns will be the direct result of small-scale dynamics. An example is a "driven" trend where all component lineages are biased toward size increase. But as structuring increases, large-scale behavior will be increasingly independent of small-scale dynamics. An example is a barrier on attainable small size that produces an asymmetrical "passive" trend wherein the maximum size of the clade increases while minimum size is unchanged. In extreme cases, structuring could control many details of clade behavior, almost irrespective of small-scale dynamics.

A classic example of clade diversification is body size evolution. This is explored by Douglas Kelt and James Brown, who expand a model proposed by Brown and others (1993) based on PEF (potential energetic fitness). The PEF model predicts that the peak body size of a clade reflects the optimal size for most readily converting available energy resources into offspring. For mammals, this is about 100 g. Kelt and Brown show evidence that PEF is a major factor underlying the distribution of body sizes at local and regional scales across ecological and evolutionary time scales (see also Brown 1995).

Small-scale and large-scale dynamics of clade diversification can result from either intrinsic properties, such as developmental constraints, or extrinsic forces of environmental selection. Or, most often, such dynamics result from the interaction of both intrinsic and extrinsic forces. This interaction

is explored by Gunther Eble, who uses fossil data to test Kauffman's (1993) rugged fitness landscape model. Although Kauffman's application of self-organization to biodiversity evolution has received much theoretical attention, Eble shows that Kauffman's model does not provide a good fit to the patterns of origination of higher taxa in the fossil record. While certain regularities and similarities to the rugged fitness model do occur, Eble shows that the model may need to be refined.

The final chapter in Part One addresses the very coarse scales of turnover of higher taxa in geological time. Norman Gilinsky presents evidence of long-term decline of background family origination and extinction. This represents a decline in turnover "volatility." What causes this pattern? Part of the explanation, suggested by John Sepkoski, who has pioneered such work, is that extinction-prone clades such as trilobites have become extinct. Thus, if family turnover translates directly into species turnover, then Gilinsky infers that niche breadth may be a factor. Citing a number of previous suggestions, he notes that more specialized species tend to have higher turnover rates.

Part Two: Community Turnover: From Populations Through Global Diversity

Ecosystems and communities experience turnover at many scales of time and space (Brown 1995; Rosenzweig 1995). Kenneth Schopf and Linda Ivany present a novel view of ecosystem stasis and change that is explicitly hierarchical. Reviewing extensive data from the fossil record, they discuss how finer scales of observation tend to show evidence for fluctuating species composition of ecosystems. Such finer scales include temporal scales ranging from a few years though a few hundred thousand years. In contrast, coarser scales of study have tended to yield patterns interpreted as showing stasis. Such coarser scales include time spans on the order of a few to many millions of years. Examples of such coarse-scale stasis are Boucot's (1990a) ecological-evolutionary units, and subunits of it identified by Brett and Baird (1995). The main question is whether this stasis is real, being caused by such processes as "ecological locking," or whether it is simply an artifact from coarser scales of resolution filtering out much of the small-scale turnover (McKinney et al. 1996; Alroy, chapter 12).

Species are not randomly distributed across the earth. Alan Cutler discusses an important nonrandom pattern that may eventually reveal much about the underlying processes of origination and extinction. This is the very common pattern of "nested subsets": less species-rich biotas are composed of subsets of species of more species-rich biotas. A species absent from one biota

will tend to be absent from all smaller (less species-rich) biotas. If it is present in a biota, it will tend to be present in all of the more species-rich biotas. Cutler shows how three nonexclusive processes can produce such nestedness: (1) passive sampling, (2) nested habitat distributions, and (3) colonization/extinction. Of special interest to biodiversity dynamics is the third process. Selective extinction can produce nestedness as can differences in colonization ability. Broadly adapted species that can both resist extinction and colonize a range of habitats will be found in many subsets, of all sizes. In contrast, species specialized to a narrow range of habitats will be found only in a few subsets. Can differences in speciation and extinction, on an evolutionary time scale, explain nestedness on continental spatial scales?

The crucial issue of diversity equilibrium is supported by John Alroy's thorough study. Using a huge database, he finds cogent evidence that North American mammal diversity has been relatively constant throughout much of the Cenozoic, indicating the existence of a static equilibrial point. Origination rate is inversely related to diversity, whereas extinction rate is not, so Alroy infers that evolutionary niche saturation is the key process underlying the logistic diversity pattern observed. This conforms to the suggestion of Rosenzweig and McCord (1991) of evolutionary incumbency and niche-preemption as a main control producing equilibrial diversity patterns: As new species evolve to fill niches after a mass extinction, the number of available niches diminishes proportionately with time. The pattern seen in Alroy's data also fits data from other studies showing that origination, and not extinction, is the main control on regional and global diversity. Extinction rate plays little role, as, at geological scales, it is often relatively constant through time. Importantly, Alroy's data seem to contradict a number of other currently popular theories about diversity dynamics, such as the Red Queen, Raup's "kill curve," Vrba's "turnover pulse" hypothesis, and coordinated community stasis.

Another example of a logistic diversity pattern is also seen in Ordovician marine genera as shown by Arnold Miller and Shuguang Mao. The Ordovician experienced major evolutionary radiations of both Paleozoic and Modern marine faunas, with both genus and family diversity increasing by threefold or more. This logistic growth apparently occurred quite rapidly, even faster than previously thought (Miller and Foote 1996). Miller and Mao's work is especially illuminating because they attempt to relate this global increase in diversity to processes that were occurring at smaller spatial scales. They conclude that some scales of observation show unique patterns not visible at other scales. Thus, the global diversity signal was not simply the summed result of community-level diversification. Their interesting suggestion is that biotic factors may have been more important at local, commu-

nity scales, whereas abiotic diversity controls may have dominated at larger, paleocontinental scales.

Equilibrial community diversity patterns are also a theme in Michael Rosenzweig's stimulating and provocative discussion of species accumulation in space and time. This is an expansion of Preston's concept that a "species-time" curve is a theoretical analog to the much better known species-area curve. If true, it would imply a dynamic where horizontal (spatial) division of habitat is similar to vertical (temporal) division of habitat. Rosenzweig discusses evidence that species do in fact temporally accumulate in an apparently regular way, at both regional and global spatial scales. Based on the rate of turnover in the accumulation curves, Rosenzweig infers that species turnover in evolutionary time is similar to the rate of species turnover seen spatially among major geographic provinces. In contrast, space and time do not seem to be as interchangeable at smaller, ecological scales. However, there is evidence for a regular temporal accumulation in paleocommunities in local stratigraphic sections (see McKinney 1996a; McKinney et al. 1996). One of the most contentious of Rosenzweig's findings is that long-term speciation rates over the last 500 million years may have been relatively constant [see e.g., Gilinsky (chapter 9) and Alroy (chapter 12)].

Evolutionary equilibrium indicates that there is a balance between speciation and extinction. A main benefit of studying evolutionary turnover is that we are in a much better position to understand the origins of biodiversity rather than just its maintenance. Compared to studies of biodiversity maintenance in a community, the origins of that biodiversity have been greatly neglected. This is the central point made by Warren Allmon, Paul Morris, and Michael McKinney in their intermediate disturbance hypothesis of maximal speciation. They discuss both fossil and modeling evidence for this hypothesis, which proposes that maximum rates of speciation will be produced at intermediate levels of disturbance. Very high levels of disturbance will result in extinction, stress, and depauperate faunas, whereas very low levels will not provide the environmental stimuli that drive natural selection. This hypothesis has an obvious connection to the older notion that intermediate disturbance maintains higher levels of diversity (e.g., Petraitis et al. 1989), but it explicitly addresses the very different process of diversity origination. The turnover dynamic of extinction is thus balanced by speciation and not immigration.

Turnover at many scales has generally been underappreciated by both ecologists and evolutionary biologists. Gareth Russell suggests that similar approaches can be used to study turnover at any level in the hierarchy of life, including turnover in time and space. The general principles that emerge are an important link between ecology and evolutionary biology. While ecolo-

gists have focused on turnover at fine spatiotemporal scales and evolutionary biologists have focused on coarser spatiotemporal scales, Russell shows that similar patterns and processes occur at both ecological and evolutionary scales. While it has long been recognized that species origination and extinction are analogous to population immigration and local extinction (e.g., MacArthur and Wilson 1967), Russell rigorously quantifies interpretation and modeling of this analogy. The result is that spatiotemporal turnover in “time-averaged” paleocommunities can be studied to describe how cumulative ecological turnover is translated into long-term ecological and evolutionary turnover (also see McKinney and Allmon 1995).

We might expect that turnover at many scales can be related to fluctuations in nutrient levels, biomass, productivity, and other ecosystemic properties. Evidence from fossil and living marine biota, as Ronald Martin discusses, indicates that changes in nutrient levels may have played a major role in many mass (and minor) extinctions. A counterintuitive insight of his view is that increased productivity can accompany extinction at many scales. This period of destabilization is followed by reequilibration to new conditions, which is often characterized by increased biomass and biodiversity. The result, as Martin discusses, has been a long-term global increase in biodiversity, the complexity of ecosystems, and such ecosystemic properties as biomass and productivity. Increased nutrient input, at many scales, may thus cause a temporary surplus of extinction over origination, but leading to a greater accumulation of species in the long term.

Patterns of change are often related to scale of observation, as discussed in Schopf and Ivany’s paper above. A basic message of Richard Aronson and Roy Plotnick is that both scale-dependent and scale-independent patterns and processes occur in biological dynamics. However, in seeking emergent properties unique to just one level, scale-independent processes have often been overlooked. Physical disturbances, for instance, have a strong influence on community, and taxic turnover may operate at a similar fashion at many or all scales. Some biotic traits such as extinction resistance may operate similarly at all scales from that of individual death, through population, and up through species and even higher taxa (see also Harrison’s chapter and the preceding discussion of it). Aronson and Plotnick note that, in such cases, long-term community and taxic patterns may simply result from the summed, additive effects of small-scale processes rather than any synergistic interactions such as “ecological locking” within communities.

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