

A null biogeographic model for quantifying the role of migration in shaping patterns of global taxonomic richness and differentiation diversity, with implications for Ordovician biogeography

Noel A. Heim

Abstract.—Biodiversity patterns in the fossil record are often interpreted as functions of only origination and extinction whereas the migration of taxa among regions or paleocontinents is rarely considered. A null biogeographic model is presented that evaluates the role of migration in shaping global biodiversity patterns across evolutionary time scales. As taxa are allowed to originate, go extinct, and migrate among continents, the model keeps track of global richness and differentiation diversity (the diversity gained by pooling continents). The model's results highlight the difference between global-scale and continental-scale origination and extinction rates. Intuitively, origination and extinction have opposite effects on global richness at the global scale, but they interact with migration at the continental scale to influence differentiation diversity and global richness in surprising ways. The model shows that the migration of taxa among paleocontinents can facilitate an increase in global richness, even when continental extinction is greater than continental origination. Additionally, the model shows that differentiation diversity reaches a dynamic equilibrium that is dictated by the combination of migration, origination, and extinction rates. A test of the model with Ordovician macroinvertebrate data indicates that migration rates were low during the Ordovician and that differentiation diversity was high and varied little. Overall, the Ordovician was an interval of high provinciality. It also shown that widespread genera were less prone to global extinction, even though extinction of genera on individual paleocontinents was common.

Noel A. Heim. *Department of Geology, University of Georgia, Athens, Georgia 30602.*
E-mail: naheim@uga.edu

Accepted: 31 January 2008

Introduction

Understanding the history of Phanerozoic biodiversity is a major goal of paleobiology. To this end, many studies of Phanerozoic biodiversity have focused on the dynamics of origination and extinction (e.g., Gilinsky and Bambach 1987; Gilinsky 1994; Patzkowsky 1995; Foote 2000, 2003; Jablonski 2001; Stanley and Powell 2003; Bambach et al. 2004). However, the migration of taxa from the regions in which they originate to other regions plays a key role in shaping regional and global biodiversity. Knowing the role migration plays in shaping biodiversity over evolutionary time scales is necessary for a complete understanding of diversity patterns observed in the fossil record. Such an understanding may also be useful to conservation biologists who need to predict the long-term evolutionary impacts of invasive species, whose migration potential is increased by anthropogenic activities (e.g., Elton 1958; Stachowicz et al. 1999; Mooney and

Cleland 2001). Null models provide simple hypotheses that require a minimum number of parameters to explain observations (Gotelli and Graves 1996) and in the past, null models have been used to evaluate migration and local extinction (MacArthur and Wilson 1967). A null biogeographic model is presented here that examines how migration interacts with origination and extinction to affect changes in differentiation diversity and global richness.

Many studies of biodiversity at the global scale (e.g., Sepkoski 1981; Sepkoski et al. 1981) have not fully considered the role of migration (for an exception, see Jablonski et al. 2006). This is likely because origination and extinction have typically been viewed as sufficient to explain global richness patterns. However, global richness is not the simple sum of its paleogeographic regions (Sepkoski 1988; Miller and Mao 1998). The proportion of widespread taxa exerts an important control on global diversity, and taxa typically become widespread through migration. Thus, when collecting

data for more than one discrete region, it is necessary to address differentiation diversity (Whittaker 1977), which is a measure of the diversity gained by pooling samples. The present model simulates biodiversity on three continents as a function of migration, origination, and continental extinction. It is important here to distinguish between different levels of extinction. This model is concerned primarily with continental extinction, which is the loss of all populations of a taxon on a continent. Continental extinction is distinguished from the loss of all populations (global extinction) and the loss of a single population (localized extirpation). Examining combinations of the model parameters allows the effects of each parameter on global richness and differentiation diversity to be isolated from the others.

Methods

Differentiation Diversity.—To help better understand the scales of biodiversity, Whittaker (1977) outlined two broad categories of diversity metrics that can be applied to multiple spatial scales: inventory diversity and differentiation diversity. Inventory diversity measures diversity at a single spatial scale whereas differentiation diversity measures diversity between two spatial scales. The most commonly used level of differentiation diversity in the paleontological literature is beta, which is the difference among environmentally homogenous local communities (alpha) within a single landscape (gamma). Beta diversity is the diversity gained by pooling multiple local samples to form a single regional sample. However, the scales of interest for the present study are continental and global; the model presented below simulates delta diversity (Whittaker 1977), rather than beta diversity. The reintroduction of delta diversity here is warranted. Previous studies of differentiation diversity of the Phanerozoic fossil record have focused on local fossil collections (Kowalewski et al. 2002; Layou 2007; Patzkowsky and Holland 2007), even when they are pooled over continental or global scales (Sepkoski 1988; Miller and Mao 1998). Beta and delta are both forms of differentiation diversity; the difference between the two is the spatial scale to

which they are applied. Although the computations of beta and delta are identical, ecological and evolutionary processes operate differently at different spatial scales (Okuda et al. 2004), and beta and delta may vary independently. This study focuses on genus lists compiled for entire paleocontinents, not local collections. Therefore, delta diversity is the measure of differentiation diversity used here. The specific measure of delta diversity used in the model is based on the Jaccard coefficient of similarity. In order for greater values of delta diversity to reflect greater differences, delta is calculated as one minus the Jaccard coefficient,

$$\delta = 1 - S_c / (S_1 + S_2 - S_c) \quad (1)$$

where S_1 is the number of taxa in assemblage one, S_2 is the number of taxa in assemblage two, and S_c is the number of taxa in common to both assemblages. Delta varies from a maximum of one, when no taxa are shared, to a minimum of zero, when both assemblages are identical.

The Jaccard coefficient has a long history as a diversity metric in the paleontological literature (e.g., Cheetham and Hazel 1969; Sepkoski 1974, 1988; Miller and Mao 1998; Shen and Shi 2004). The advantages to using the Jaccard coefficient are that it is a simple and direct measure of similarity (i.e., percentage of shared taxa), and it relies on presence/absence data rather than abundance data. One problem with the Jaccard coefficient is that it is sensitive to differences in the sizes of the samples being compared. However, sample-size dependence cannot be avoided with many commonly used metrics that do not consider abundances (Wolda 1981). The sample sizes (i.e., number of genera) for the model are approximately equal for all continents, and no sample-size bias is imposed on the results.

The Model.—The model presented here tracks changes through time in global richness and delta diversity among continents as taxa are randomly allowed to undergo origination, extinction, and migration among three continents. The fundamental evolutionary unit considered here is the denizen, used in the general sense as a taxon that occupies a region or continent. Each taxon on each continent

represents a single denizen. At each time step, the action of each denizen is determined by three model parameters: the probability of migration to another continent (p_m), the probability of origination (p_o), and the probability of extinction on a continent (p_e). The latter two parameters correspond to continental, not global, rates of origination and extinction. The three parameters do not necessarily sum to one, allowing the possibility of no change during a time step. An important quantity in the model is the ratio of the probability of origination to the probability of extinction, called inflation (p_o/p_e). Inflation indicates how the richness of a continent will change in the absence of migration. When inflation is equal to one ($p_o = p_e$), continental origination and continental extinction balance each other and any net changes in continental richness is the result of migration. When inflation is less than one ($p_o < p_e$), the net richness of a continent will decrease unless migration replaces extinct taxa with immigrants. When inflation is greater than one ($p_o > p_e$), migration will combine with origination to induce a net increase in the richness of a continent.

For the purposes of this model, migration is defined as the dispersal to, and successful establishment of, a taxon on a new continent while remaining present on the original continent. Migrating taxa are increasing their geographic range. In this null model, all denizens are equal with respect to the model parameters. Additionally, the model parameters are not independent. If a denizen undergoes a change during a time step, the probability of the other two parameters automatically becomes zero for that denizen during that time step; a denizen will undergo not more than one change during a single time step. This is an oversimplification of real-world possibilities because all three pairwise parameter combinations are theoretically possible within a single time step. For example, a denizen could migrate to establish that taxon elsewhere and go extinct locally during the same time step. However, allowing for such scenarios increases the model's complexity, possibly beyond our current ability to accurately document them in nature. For example, if simultaneous migration and extinction are allowed, should

simultaneous origination and extinction be allowed? Allowing for the complete independence of all three parameters introduces unwieldy complexities, particularly with respect to extinction. In this model there are continental and global rates of extinction. Continental extinction is explicitly defined in the model, and global extinction results from one or more random continental extinction events. If simultaneous origination and extinction, potentially interpretable as phyletic extinction, is allowed, then four levels of extinction need to be tracked—continental and global for both phyletic and non-phyletic extinction. Tracking phyletic extinctions in the fossil record at global and continental scales requires detailed phylogenies that are presently not available for most taxa. For the time being, the most useful model has dependence among the three parameters rather than selective independence among some pairs and dependence among others. As more data for testing this new approach to biodiversity dynamics become available, more sophisticated models will certainly be developed. For now the simple null hypotheses generated by this model are most appropriate for the available data.

Each model run consists of 15,000 time steps of 10 Kyr each; the total duration of each run is 150 Myr. The model includes 405 trials covering all combinations of the discrete values of p_m , p_o and p_e used in the model (see Appendix 1 online at <http://dx.doi.org/10.1666/07043.s1>). Model parameters are fixed within each run, but they vary among runs with continental rates of 0.0001 per Myr to 1.0 per Myr. Continental origination and extinction rates are calculated for a data set of Ordovician marine invertebrates (see "Application of Null Model"), which bracket the rates used here.

Global diversity at the beginning of each model run (t_0) is 100 taxa. These taxa are assigned to continents by scrolling through the taxon list and randomly assigning each taxon to exactly one of the three continents. This ensures that each continent contains a unique, endemic fauna at t_0 . The model was also run with initial conditions of three identical continental faunas at t_0 ; there was no difference in results, which are not shown here. At each time step, each denizen will do one of the fol-

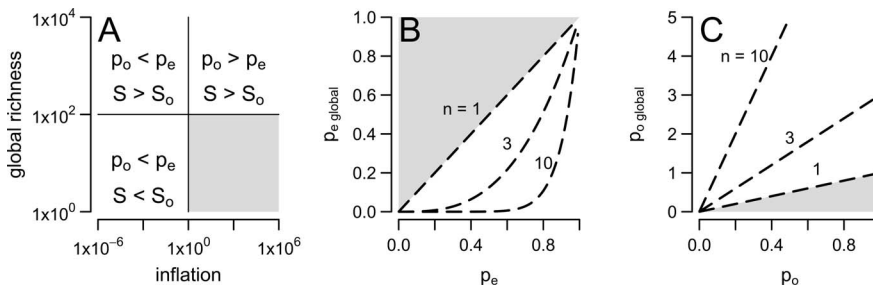


FIGURE 1. Schematic representations of the relationships among continental extinction (p_e), continental origination (p_o), and global richness. In all plots the shaded regions represent impossible values. (A) The relationships between inflation (p_o/p_e) and increases in global richness. S_0 is the initial global richness. The vertical line marks where the rate of origination equals the rate of extinction. The horizontal line represents global richness at t_0 , 100 taxa. (B) Differences between continental and global extinction rates as taxa become more and more widespread. n = the number of continents on which a taxon exists. When $n = 1$, global extinction equals continental extinction. Global extinction is always less than or equal to continental extinction. Note that the rate of extinction can never be greater than one. (C) Differences between continental and global origination rates as taxa become more and more widespread. When $n = 1$, global origination equals continental origination. Global origination is always greater than or equal to continental origination, and rates greater than one are possible.

lowing: (1) expand its range to include another continent, (2) go extinct on the continent on which it is being evaluated, (3) generate a new taxon (origination) on the continent on which it is being evaluated, or (4) remain unchanged. A key aspect of the model is that taxon occurrences on each continent (i.e., denizens) are evaluated independently. For example, a single taxon could migrate from one continent to a second and be extirpated from a third in the same time step.

At the end of each model run, global richness and the richness of each continent are tabulated. Also, delta diversity is calculated for each combination of two continents and the mean pairwise delta diversity of all three is computed. The mean delta diversity is one at t_0 because each continent starts with a unique set of endemic taxa. In approximately 73% of the runs, the average delta diversity reaches a dynamic equilibrium (see “Model Results”). The equilibrium delta diversity (δ_{eq}) and equilibrium time, the time it takes to reach equilibrium, are estimated for each run by fitting a logistic curve to a time series plot of global average delta. The logistic curve is fit using the *SSlogis* function in the software package *R* (R Core Development Team 2006). The fit logistic function has the following form:

$$f(t) = A/(1 + e^{(m-t)/r}), \quad (2)$$

where A is the asymptote, m is the location of

the inflection point, and r is a fit constant. The equation parameters are fit to the data by using the least squares method. The equilibrium delta diversity (δ_{eq}) is the asymptote of the fit logistic curve, and the equilibrium time is designated as the first time step in which the global average delta is within two standard errors of the asymptote. See the Appendix 1 for δ_{eq} values with standard errors.

Model Results

Migration and Global Richness.—Migration of taxa among continents has an important impact on global richness. A critical quantity that emerges from the model is inflation (p_o/p_e). If migration is set to zero, global richness is always less than or equal to the initial richness when inflation is less than one (i.e., $p_o < p_e$), and global richness is always greater than or equal to the initial richness when inflation is greater than one (i.e., $p_o > p_e$). However, if migration is non-zero, there are instances when inflation is less than one and global richness is greater than the initial richness, especially as the fauna ages (Fig. 1A, Fig. 2). Keep in mind that p_o and p_e are continental, not global, rates. When continental extinction outpaces continental origination and the migration rate is the maximum considered here (1 Myr^{-1}), global richness begins to increase within 10 Myr. Over a duration of up to 150 Myr, migration rates as low as 0.01 Myr^{-1} may induce an increase in global richness under similar

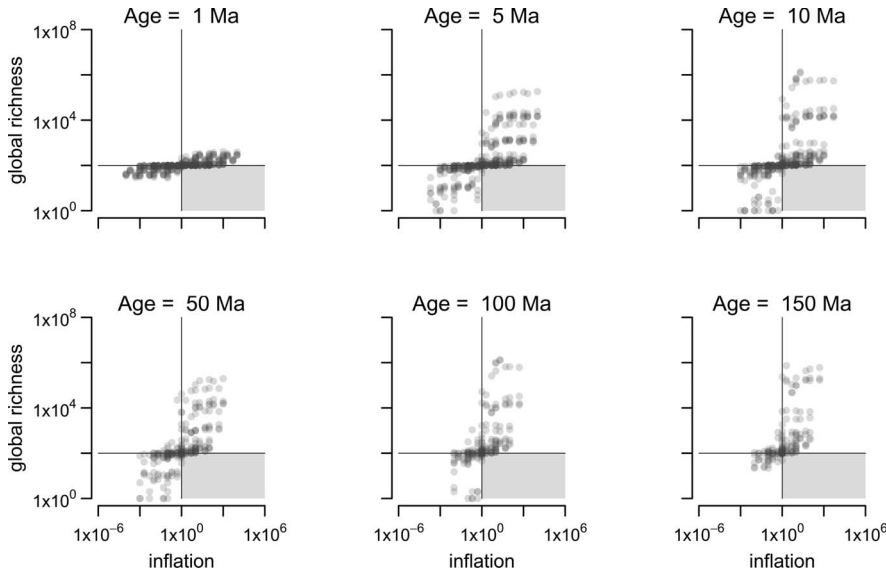


FIGURE 2. Global richness plotted against inflation (p_o/p_e) for all 405 runs of the model at six time intervals after t_0 . These plots are set up the same as in Figure 1A. The points are shaded so that overlapping points are darker. In all panels, the rate of migration is non-zero. Note that when inflation is greater than one, global richness is always greater than or equal to the initial richness of 100, but when inflation is less than one, global richness is sometimes greater than 100 because migration increases the global origination rate above p_o and decreases global extinction below p_e .

conditions of continental origination and extinction. Increasing global richness when continental extinction outpaces continental origination highlights the difference between continental and global rates. The difference between continental and global rates arises because the denizens of a single taxon on separate continents are evaluated independently. In order for a taxon that occurs on more than one continent to go extinct globally, it must go extinct independently on all continents. Thus, the probability of global extinction is less than that of continental extinction and is given by

$$p_{e\ global} = p_e^n, \quad (3)$$

where p_e is the probability of continental extinction and n is the number of continents on which the taxon occurs. It is true that $p_{e\ global} \leq p_e$ for all possible values of p_e (Fig. 1B). Extinction must be less than or equal to one, otherwise there would be more extinction events than available denizens. The probability of global origination for a taxon occurring on multiple continents is greater than that for continental origination because there are multiple independent chances to produce a

daughter taxon. The global origination probability is given by

$$p_{o\ global} = p_o \times n, \quad (4)$$

where p_o is the probability of continental origination. It is always true that $p_{o\ global}$ is greater than or equal to p_o (Fig. 1C). As a taxon becomes more widespread with increasing migration rate, the chance of global extinction is reduced, and the chance of origination is increased, allowing global richness to increase despite continental extinction being greater than continental origination (Fig. 2).

Migration and Delta Diversity.—The migration of taxa among continents also influences delta diversity. Because the model begins with three continents containing endemic faunas, delta diversity will remain at one (δ_0) if there is no migration. The null expectation is maximal differentiation, so delta diversity can only decrease from δ_0 as migration is allowed to vary, and it does so in several ways. The best way to visualize the influence of migration, origination, and extinction on delta diversity is through bivariate plots of delta diversity versus the probability of continental

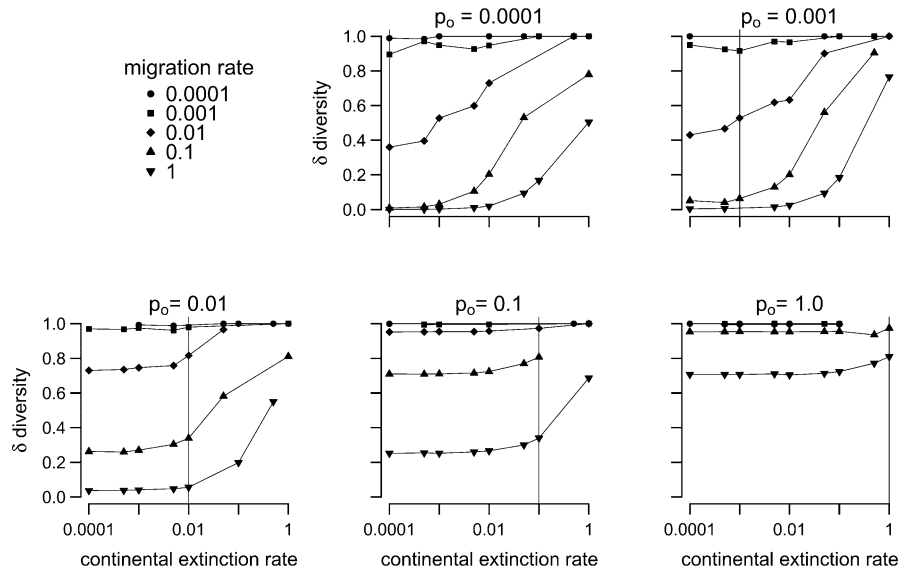


FIGURE 3. Bivariate plots of delta diversity versus extinction rate. Delta is computed as one minus the Jaccard coefficient. Each plot area is for a different continental origination rate (p_o) and the symbols represent different migration rates. All rates have units of Myr^{-1} . The vertical line marks where the rate of origination equals the rate of extinction.

extinction for each level of continental origination (Fig. 3). Several general patterns emerge from the modeled delta diversity. First, increasing migration reduces delta diversity relative to δ_o . As increased migration makes the taxonomic composition of the continents more similar, delta decreases for any given combination of continental origination and extinction. Second, increasing the rate of continental origination counteracts the influence of migration by adding new endemics, thus increasing delta diversity. Third, negative inflation (i.e., $p_o < p_e$) also counteracts migration for any given combination of migration and origination. Because continental extinction is greater than continental origination, the world will be populated with older, widespread taxa. The extinction of denizens belonging to widespread taxa will increase delta diversity. Fourth, delta diversity reaches a steady state for all values of migration when the rate of continental origination is greater than the rate of continental extinction. The steady state in delta diversity is generated by a balance between origination and migration. Because continental origination is greater than continental extinction, new endemic taxa have time to migrate to other continents before be-

coming locally extinct. In this situation, continental extinction is neutral with respect to delta diversity. Because there is a mixture of widespread and endemic taxa, the continental extinction of the former increases delta diversity while the extinction of the latter decreases delta diversity. These patterns emphasize the fundamental difference between continental origination and extinction as evolutionary processes. All originations increase delta diversity, whereas the extinction of a denizen may increase or decrease delta diversity. Similarly, all originations increase global richness, whereas the extinction of a denizen may or may not decrease global richness.

Approximately 27% of the 405 model runs fail to reach a dynamic equilibrium in delta diversity within 150 Myr (Fig. 4). Equilibrium is not reached for the full range of migration when inflation is less than one ($p_o < p_e$) and extinction is greater than about 0.1 Myr^{-1} . When extinction greatly outpaces origination, the residence time of immigrant taxa is too short for an equilibrium to be reached quickly. Also, equilibrium is not reached within 150 Myr for low levels of migration when inflation is greater than one ($p_o > p_e$). With low rates of migration, it is expected that an equilibrium

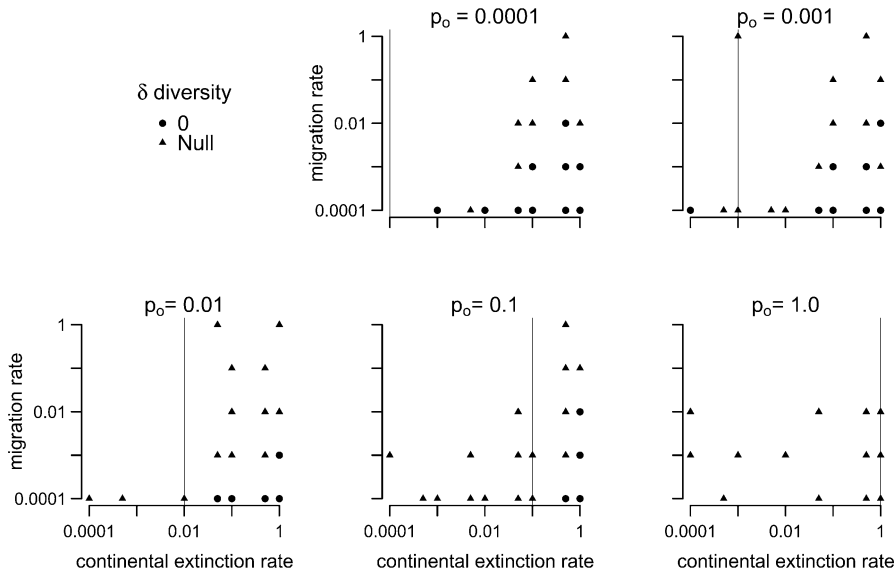


FIGURE 4. Bivariate plots of the migration rates versus continental extinction rate for those model runs whose δ_{eq} value is one (circles) or δ_{eq} is never reached (triangles). Each plot area is for a different continental origination rate (p_o).

will be reached slowly, even with high origination. Delta diversity remains maximal when the rate of extinction is high and the rate of migration is low, except for the highest levels of origination. Combining the highest extinction and lowest migration rates inhibits taxa from spreading to new continents.

An important aspect of this model is the equilibrium time. Equilibrium times are determined primarily by continental origination and migration; extinction has little effect on the equilibrium time in most cases (Fig. 5). As with δ_{eq} , continental extinction appears to be neutral, and a balance between continental

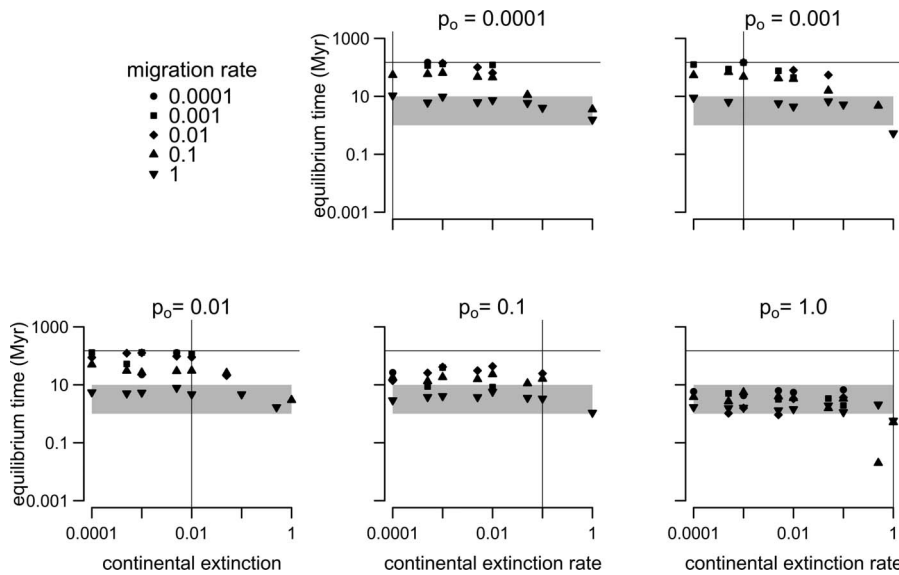


FIGURE 5. Bivariate plots of the equilibrium time versus continental extinction rate. Each plot area is for a different continental origination rate (p_o) and the symbols represent migration rates. The vertical line is the same as in Figure 3. The horizontal line is at 150 Myr, the maximum time the model can simulate. The shaded regions indicate equilibrium times between 1 Myr and 10 Myr, which bracket the average Phanerozoic stage duration.

origination and migration is reached. Lower levels of migration produce longer equilibrium times. As the level of origination increases, the equilibrium time tends to decrease. For nearly all runs with continental origination rates greater than 0.1 Myr^{-1} , the equilibrium time is less than 10 Myr (Fig. 5).

Discussion of the Model

Migration and Global Diversity.—The results of this model show that the migration of taxa among continents influences global richness. Because of this, explicitly including migration as an evolutionary parameter in future studies of evolutionary rates is warranted. The typical data set from which global Phanerozoic origination and extinction rates are calculated contains a list of genera with some estimate of the timing of global first and last appearances (e.g., Sepkoski et al. 2002). However, this type of data set excludes vital geographic information that is necessary for estimating migration rates and continental rates of origination and extinction. These model results highlight a fundamental difference between global and smaller-scale, in this case continental, rates of origination and extinction. Under conditions of non-zero migration, global richness may increase, while continental rates of extinction are higher than those of continental origination. Although Miller and Mao (1998) didn't calculate origination and extinction rates, this result corroborates their conclusion that continental dynamics need not exhibit a one-to-one correspondence with global dynamics. Furthermore, the model results suggest that migration can play a role in increasing global richness. The nature of the model does not allow for a direct assessment of the relationship between global richness and migration, but there is an inferred positive relationship based on the influence of migration on global origination and extinction rates (eqs. 3 and 4). However, the positive relationship at this point is speculative. Migration could also decrease global diversity. If three continents each have 100 taxa and delta diversity is high because of high migration, global richness will be greater than if delta diversity and migration are low. Despite the ambiguity of migration's role in determining global richness, the

model results suggest that global richness is driven primarily by origination. Migration is likely to have an important influence on global richness only when continental extinction rates are low relative to origination and migration rates are high.

Migration and Delta Diversity.—The model results for delta diversity (Fig. 3) highlight migration as a process that reduces delta diversity, continental origination as a process that increases delta diversity by counteracting migration, and extinction as a process that can either increase or maintain differentiation diversity, depending on inflation. Migration reduces delta diversity by increasing the taxonomic similarity among continents, an unsurprising result. The immigration of a new taxon will increase the richness of that continent while making the difference between the continents less. This suggests that intervals of high provinciality should be characterized by low rates of migration. This is consistent with an increase in late Paleozoic provinciality (Bambach 1990), which has been attributed to reduced geographic range of taxa (possibly from reduced migration) rather than increased endemism (possibly from increased origination). The role of continental extinction in determining delta diversity is more ambiguous than that of migration and origination. The ambiguous role of continental extinction in diversity dynamics is manifest in the response of δ_{eq} to inflation; delta diversity remains at a steady state while extinction is less than origination, but rapidly approaches δ_0 as extinction becomes greater than origination, especially for the highest rates of migration (Fig. 3). This result is somewhat surprising, particularly the stability of δ_{eq} when inflation is less than one. Because the extinction of a continental denizen will decrease delta diversity if the denizen is endemic and will increase delta diversity if the denizen is of a widespread taxon, the overall effect of extinction depends on the proportion of endemic and non-endemic taxa on a continent. If there is a mix of widespread and endemic taxa then continental extinction is neutral with respect to delta diversity. But, if most taxa are widespread, then continental extinction increases delta diversity. The interpretation of these ex-

tion dynamics is surprising, but preliminary. Further theoretical and empirical exploration of how extinction influences biodiversity dynamics at multiple spatial scales should yield interesting and more definite results.

The time it takes the model to reach an equilibrium in delta diversity ranges from less than 1 Myr to more than 150 Myr. For the range of origination rates in this model, many of the equilibrium times are between 1 and 10 Myr. Many paleontological data sets are binned chronologically by stages. The average post-Cambrian stage has a duration of 5.7 Myr (Gradstein et al. 2004), which means that calculations of delta diversity for individual stages potentially reflect equilibrium values, especially if rates of continental origination and migration are greater than about 0.1 Myr⁻¹ (Fig. 5). The assumption of equilibrium at the stage level will not necessarily be easy to verify. High-resolution stratigraphic information is required to observe an asymptotic, logistic increase in delta diversity through a stage. Such data may be available from detailed regional field studies, but the correlation of individual collections across continents is not likely for any substantial portion of the Phanerozoic record. Although the demonstration of equilibrium in delta diversity is unattainable for large spatial scales across intervals of geologic time, the assumption of equilibrium may be reasonable if observed rates are large enough.

Delta Diversity and Mass Extinctions.—The steady state in delta diversity when origination is greater than extinction and the increase in delta diversity as origination becomes greater than extinction (Fig. 3) may have important implications for understanding Phanerozoic extinction events. Indeed, Jablonski (1998) found that the proportion of invasive (i.e., migrating) genera immediately following the end-Cretaceous extinction varied among continents. Bambach et al. (2004) recognized two categories of mass extinction events: true mass extinctions characterized by elevated extinction rates and mass depletions characterized by reduced origination rates. The model results suggest that delta diversity will change differently for each type of extinction. Consider a hypothetical situation where the

rates of origination and extinction are equal and migration is at a high level but constant. During a mass extinction event where the continental extinction rate is elevated above the continental origination rate, delta diversity will increase precipitously. However, during a mass depletion where the origination rate drops below the extinction rate, delta diversity will decrease. Continuing with the same hypothetical system with initially equal continental origination and extinction rates and constant migration, changes in delta diversity can also be predicted for radiation events. If origination increases from its initial state, delta diversity should increase. Finally, if the rate of extinction drops below the rate of origination, no change in delta diversity is expected. This last scenario generates exponential diversification with constant origination that is not balanced by extinction. These hypotheses have yet to be tested, but they represent a potentially fruitful new direction in paleoecological research.

With the emergence of high-quality paleogeographic maps (Scotese 2001) and global-scale databases, such as the Paleobiology Database (<http://pdb.org>), that contain paleogeographic and paleoenvironmental information, it is now possible to track not only global richness and global origination and extinction rates through time, but also migration and continental origination and extinction rates. With paleogeographic information for each taxon occurrence in a database, migration rates can be calculated by comparing the timing of a taxon's global first occurrence with each of its continental first occurrences. Continental extinctions can be calculated by comparing global last occurrences with continental last occurrences. Origination, of course, is not scale dependent; the continental origination of a taxon is also its first global occurrence. Understanding the macroevolutionary role of migration in the history of Phanerozoic biodiversity represents a new and important direction for paleobiological research.

Application of Null Model

Ordovician Data.—This biogeographic model of migration is applied to a data set of Ordovician benthic macro-invertebrates extract-

ed from the Paleobiology Database (PBDB). The full data set consists of 9187 genus occurrences, 1147 unique genera, and 1993 collections (data are stored online with the PBDB under Official Publication 71 at <http://www.paleodb.org/>). Following Miller and Mao (1998), the data set is composed of the Trilobita, Brachiopoda, and the molluscan classes Monoplacophora, Bivalvia, and Gastropoda. Using only benthic groups standardizes the ecological and life history traits by excluding groups such as nektonic cephalopods that spend the entirety of their life in the water column above the sediment-water interface and are largely viviparous (Ruppert and Barnes 1994). Additionally, these taxa are chosen because they represent a cross section of Ordovician marine invertebrates and all three evolutionary faunas (Sepkoski 1981). The data are stratigraphically binned into the PBDB's five default bins for the Ordovician, corresponding to the Tremadocian, Arenigian, combined Llanvirnian and Llandeilian, Caradocian, and Ashgillian stages of the standard British time scale. Additionally, data from the youngest Cambrian and oldest Silurian bins are included so evolutionary rates can be calculated for all Ordovician bins. The data for each bin are subdivided into three paleogeographic regions: Laurentia, South China, and all other Ordovician paleocontinents. Laurentia and South China have sufficient numbers of collections in the PBDB to be analyzed separately. The remaining data are combined so that more accurate rates of origination, extinction, and migration can be calculated. As more data become available from other paleocontinents, a more realistic paleogeographic division of the data can be applied. In order to standardize the stratigraphic scale of the collections used, only collections made at the levels of bed or group of beds are included. This prevents a bias from long formation-level species lists that are common for Laurentia, but rare for South China. The other paleocontinent data from the Ashgillian has the smallest number of collections; diversity is calibrated to this level.

Ordovician Biodiversity.—Simple genus richness is calculated for each time bin, and a subsampling routine is used to account for differ-

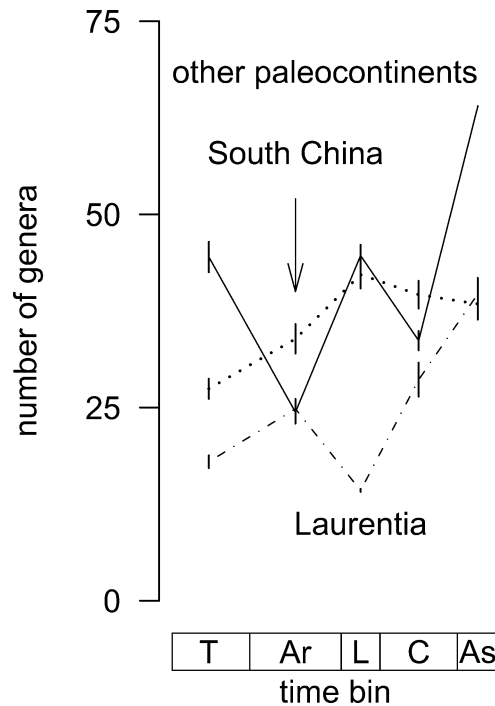


FIGURE 6. Subsampled Ordovician generic richness. Richness is calculated within each bin from 100 subsamples drawn by the by-list unweighted method (Alroy 2000; Bush et al. 2004). The time bins are the default Paleobiology Database bins for the Ordovician and correspond to the standard British time stages: T, Tremadocian; Ar, Arenigian; L, combined Llanvirnian and Llandeilian; C, Caradocian; As, Ashgillian. Each curve is for a different paleogeographic region: Laurentia (dot-dash), South China (dotted), and the combination of all other paleocontinents (solid). Vertical bars are 95% confidence intervals about the means of 100 subsamples.

ences in sampling intensity among time bins and paleocontinents. The data are subsampled using the by-list unweighted method (Alroy 2000; Bush et al. 2004) whereby the same number of collections (i.e., taxon lists) are randomly drawn without replacement from the pool of all collections, and the number of unique genera is tabulated. The unweighted method is used here because it assumes that differences in list length are real and not an artifact of sampling intensity (Bush et al. 2004). Because long formation-level lists were excluded from the data set, a weighted subsampling method would obscure real differences in list lengths.

Genus richness curves are generated for Laurentia, South China, and the pool of all other paleocontinents (Fig. 6). Genus diversity

in South China increased through the Llanvirnian/Llandeilian then remained constant through the Ashgillian. The major feature of the Laurentian curve is a marked decrease in richness in the Llanvirnian/Llandeilian that interrupts an overall increase in richness. This large drop in diversity in the Llanvirnian/Llandeilian is likely due to the Knox unconformity seen throughout eastern and central North America (Mussman and Read 1986). The curve for the other paleocontinents is volatile and shows no trend. This is likely due to the lumping of geographically disparate regions that are variably sampled within the PBDB. Presently, controlling for depositional environment is not possible because none of the Llanvirnian/Llandeilian collections from Laurentia have diagnostic environmental information.

Origination and Extinction Rates.—As described above, origination and extinction rates can be calculated at the global or continental level. Both levels of origination and extinction are calculated for the Ordovician data (Fig. 7). In calculating global rates, all stratigraphic gaps between first and last global occurrences are filled. For continental rates, it is assumed that each taxon has a continuous range on any given paleocontinent; all gaps between the first and last occurrences are filled on each paleocontinent. This assumption is parsimonious and avoids complicated histories wherein a genus is present on a paleocontinent, migrates to another paleocontinent, is extirpated from the original paleocontinent, and finally migrates back to the original paleocontinent.

Per-interval extinction rates are calculated as the ratio of the number of genera with their last occurrence in a bin to the total number of genera in that bin. Per-interval origination (and migration) rates are calculated as the ratio of the number of originations (or migrations) within a bin to the number of genera that crossed the lower boundary of that bin. Both continental and global origination rates (Table 1, Fig. 7) are maximal during the Tremadocian and decrease through the Llanvirnian/Llandeilian. Following an increase in the Caradocian, origination rates reach their minimum during the Ashgillian. Continental and global extinction rates are constant during the

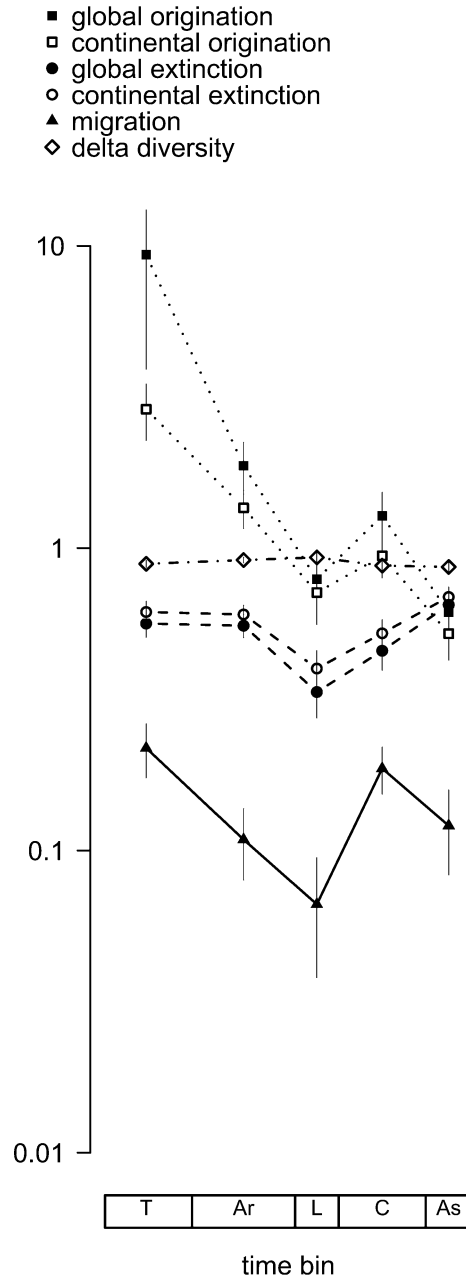


FIGURE 7. Per-time-bin origination, extinction, and migration rates for the Ordovician data. Closed symbols are global rates and the open symbols are continental rates. Also plotted is delta diversity, which is computed as the global average Jaccard among the three paleogeographic regions: South China, Laurentia, and all other paleocontinents. The time bins are the same as in Figure 6. All curves are based on means of 1000 bootstraps. Vertical bars are 95% confidence intervals.

TABLE 1. Per-time-bin origination, extinction, and migration rates for the Ordovician. Origination and migration rates are calculated as the ratio of the number of new genera (newly originated or immigrants) in a time bin to the number of genera that cross the lower boundary of that bin. Extinctions are calculated as the ratio of the number of extinctions in a bin to the total number of genera in that bin. See the text for the distinctions between continental and global rates. All rates are mean values based on 1000 bootstraps.

	Tremadocian	Arenigian	Llanvirnian/ Llandeilian	Caradocian	Ashgillian
Migration	0.22 ± 0.044	0.11 ± 0.029	0.07 ± 0.028	0.19 ± 0.033	0.12 ± 0.038
Global origination	9.35 ± 5.448	1.87 ± 0.364	0.79 ± 0.183	1.28 ± 0.250	0.61 ± 0.129
Continental origination	2.88 ± 0.609	1.36 ± 0.198	0.71 ± 0.153	0.94 ± 0.146	0.52 ± 0.095
Global extinction	0.56 ± 0.056	0.55 ± 0.048	0.33 ± 0.060	0.46 ± 0.063	0.65 ± 0.050
Continental extinction	0.61 ± 0.052	0.60 ± 0.040	0.40 ± 0.058	0.52 ± 0.057	0.69 ± 0.043

early Ordovician, drop to their minimum in the Llanvirnian/Llandeilian, then increase to their maximum in the Ashgillian. Origination rates are higher than extinction rates during the Tremadocian through the Caradocian. Origination and extinction rates diverge in the Ashgillian, and extinction outpaces origination. The high rates of origination in the early Ordovician account for the Ordovician radiation, and the elevated extinction in the Ashgillian is likely a response to the end-Ordovician mass extinction.

The global and continental rates are nearly parallel for both origination and extinction. As predicted by equations (3) and (4), the global extinction rate is always less than the continental extinction rate, and the global origination rate is always greater than the continental origination rate (Fig. 7). The difference between the two extinction curves represents the difference between the extinction of denizens on paleocontinents and the global extinction of genera. However, the global and continental extinction curves may not be directly comparable and may reflect an artifact of comparing global extinctions per genus with continental extinctions per denizen. To confirm that there are real differences between global and continental extinction rates, global extinctions per genus are compared with continental extinctions per genus (not shown). For all five Ordovician bins, the number of continental extinctions per genus is greater than the global extinctions per genus. This indicates that, on average, a genus will experience at least one continental extinction before it becomes globally extinct, suggesting that widespread taxa are less prone to global extinction. The inter-

pretation of the origination curves is less straightforward. Because an origination event is the same whether it is being counted globally or within discrete geographic regions, the difference between global origination rates and continental origination rates is, at least partially, a mathematical artifact. The same number of originations is divided by either the total number of genera or the total number of continental denizens. Despite the artifactual nature of the offset, the difference between global and continental origination rates is biologically meaningful. If allopatric speciation is a common, if not the predominant, mode of speciation, then it is expected that for a single genus present on two distant paleocontinents separated by a deep ocean basin thousands of kilometers wide, as Laurentia and South China were during the Ordovician (Scotese 2001), independent divergence between the isolated denizens is expected. Although a phylogenetic analysis is needed to confirm this hypothesis, these results suggest that allopatric speciation may be a normal mode of speciation, whereby a single parent genus can give rise to multiple daughter genera through isolation on multiple paleocontinents. Although phylogenetics often considers polytomies unsatisfactory in solutions to evolutionary relationships, they may be real consequences of paleobiogeography.

Migration Rate and Delta Diversity.—Migration rate and global average delta diversity among the three paleogeographic regions are calculated for the Ordovician data (Fig. 7). Delta diversity is calculated for the Ordovician data in the same way as in the model, one minus the global average Jaccard. The migra-

tion rate is roughly parallel to origination rate through the Ordovician. Overall, delta diversity is high throughout the Ordovician and varies between 0.87 and 0.93 (Fig. 7). The Ordovician data are largely consistent with the model. The model results indicate that when origination and extinction rates are greater than about 0.05 Myr^{-1} and migration is less than about 0.01 Myr^{-1} , then delta diversity will be greater than about 0.9 (Fig. 3). This is the case for the Ordovician. Because origination is consistently greater than extinction, the variations in extinction should have no effect on delta diversity, and continental origination is fast enough to generate delta diversity values above 0.8. This is consistent with observations that the Ordovician, particularly the late Ordovician, was an interval of high provinciality (Sheehan and Coorough 1990; Jin 2001) and that provinciality was driven by high rates of origination and low rates of intercontinental migration.

In order for the model to be applied to the Ordovician data, the measured values of delta diversity need to be either shown or assumed to represent equilibrium conditions. Given the relatively low rates of per-stage migration, it is possible that observed delta diversity does not reflect equilibrium conditions. Non-equilibrium is even more likely given that the durations of the Llanvirnian/Llandeilian and Ashgillian are shorter than the other Ordovician bins. Data with high stratigraphic resolution are needed to test for equilibrium. And, even if equilibrium was reached, only the data from the stratigraphic intervals that have reached equilibrium should be used. Questions related to equilibrium certainly need to be answered before any definite conclusions can be drawn. What proportion of the Phanerozoic record is characterized by equilibrium conditions with respect to delta diversity? Is delta diversity partially or fully reset at stage boundaries or mass extinctions? As mentioned above, answering these questions at the global scale is not tractable for the time being. However, at the sub-continental and regional scales, these questions can be investigated with detailed field studies.

Miller and Mao (1998) observed a decline in beta diversity through the Ordovician, espe-

cially in South China. As indicated above, beta and delta diversities are fundamentally different and there is no reason to assume that trends in beta diversity will have any bearing on trends in delta diversity. A pattern of scale-independence within biodiversity dynamics has emerged in recent years with the increasing number of studies using additive diversity partitioning to measure differentiation diversity at multiple spatial scales (Lande 1996; Veech et al. 2002). Although conducted at sub-continental spatial scales, several studies of differentiation diversity indicate that biodiversity dynamics at one scale are independent of those at larger or smaller scales (Gering and Crist 2002; Okuda et al. 2004; Layou 2007; Patzkowsky and Holland 2007).

Miller (1997) found that the fauna aged through the Ordovician and that older genera were widespread. Taxon ages were calculated (data not shown) for the Ordovician data used here, and the percentage of endemic genera decreases from the Llanvirnian/Llandeilian through the Ashgillian. As indicated above, if origination and extinction operate randomly on denizens at the continental level, then widespread genera will be less prone to global extinction than their endemic counterparts. This suggests that being widespread is more important for avoiding global extinction than being a good competitor with other taxa for resources. This hypothesis corroborates a finding by Jablonski and Hunt (2006) that geographic range, at least for Cretaceous mollusks, is the most important factor in species survivorship. Jablonski and Hunt also found that the mode of larval development is much less important in survivorship than geographic range. If larval mode is important for long-distance dispersal and the expansion of geographic range, then it appears that the equality among taxa with respect to migration used in the model may be an accurate representation of nature.

Despite coarse temporal constraints and possible non-equilibrium conditions, the ability of the model to explain observations in the Ordovician data is remarkable. Clearly, the migration of taxa among paleogeographic regions is an important factor in the biodiversity dynamics of ancient systems. More impor-

tantly, the quantification of migration in the fossil record is tractable, even at coarse paleogeographic and temporal scales. Additionally, these results highlight the importance of analyzing rates of origination and extinction at the regional or paleocontinental levels. If origination and extinction operate on isolated denizens, and migration generates some degree of taxonomic similarity among isolated continents, then measures of global origination and extinction rates will be different from continental rates. The difference between global and continental rates, particularly for extinction, allows a more nuanced understanding of biodiversity dynamics. Of course, these results are preliminary and likely to be modified as better data become available. This new approach to studying the Phanerozoic history of evolution and biodiversity has potential to generate a more refined understanding of how macroevolution operates over large and intermediate spatial scales.

Conclusions

1. Migration is an important evolutionary process that can facilitate an increase in global richness, even when continental extinction rates are greater than continental origination rates. Migration exerts this influence on richness by increasing the global origination rate above the continental origination rate and depressing the global extinction rate below the continental extinction rate.
2. When taxa migrate among continents, delta diversity tends to reach a dynamic equilibrium, generally within 100 Myr. However, in cases where origination *or* migration rates are high (greater than about 0.1 Myr⁻¹), equilibrium is reached between 1 and 10 Myr, which brackets the average duration of a Phanerozoic stage. The equilibrium delta diversity is determined by the combination of migration, continental origination, and continental extinction rates.
3. Migration has complex interactions with continental origination and extinction to produce delta diversity. Migration reduces delta diversity and continental origination increases delta diversity. Continental extinction increases delta diversity only when there is net extinction ($p_o < p_e$). For any given combination of migration and continental origination, delta diversity reaches a steady state with respect to continental extinction rate when there is net origination ($p_o > p_e$).
4. An examination of Ordovician data parsed by paleocontinent shows that the high rates of continental origination and low rates of migration were important factors in determining delta diversity during the Ordovician. Delta diversity was relatively high during the entirety of the period, indicating consistently high provinciality.

Acknowledgments

This research was supported by a U.S. Environmental Protection Agency STAR Fellowship, the Watts-Wheeler Fund of the University of Georgia Department of Geology, and the University of Georgia Office of the Vice President for Research. I thank K. M. Layou and S. M. Holland for many fruitful discussions on differentiation diversity, migration, and programming. Comments on earlier drafts of this manuscript from S. M. Holland, S. T. Goldstein, T. D. Olszewski, L. B. Railsback, S. E. Walker, A. M. Bush, A. I. Miller, and an anonymous reviewer greatly improved the final quality of this paper. This is Paleobiology Database publication no. 71.

Literature Cited

- Alroy, J. 2000. New methods for quantifying macroevolutionary patterns and processes. *Paleobiology* 26:707–733.
- Bambach, R. K. 1990. Late Palaeozoic provinciality in the marine realm. *In* W. S. McKerrow and C. R. Scotese, eds. *Palaeozoic palaeogeography and biogeography*. Geological Society of London Memoir 12:307–323.
- Bambach, R. K., A. H. Knoll, and S. C. Wang. 2004. Origination, extinction, and mass depletions of marine diversity. *Paleobiology* 30:522–542.
- Bush, A. M., M. J. Markey, and C. R. Marshall. 2004. Removing bias from diversity curves: the effects of spatially organized biodiversity on sampling-standardization. *Paleobiology* 30:666–686.
- Cheetham, A. H., and J. E. Hazel. 1969. Binary (presence-absence) similarity coefficients. *Journal of Paleontology* 43:1130–1136.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.
- Foote, M. 2000. Origination and extinction components of taxonomic diversity: general patterns. *In* S. L. Wing and D. H. Erwin, eds. *Deep time: Paleobiology's perspective*. *Paleobiology* 26(Suppl. to No. 4):74–102.
- . 2003. Origination and extinction through the Phanerozoic: a new approach. *Journal of Geology* 111:125–148.

- Gering, J. C., and T. O. Crist. 2002. The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecology Letters* 5:433–444.
- Gilinsky, N. L. 1994. Volatility and the Phanerozoic decline of background extinction intensity. *Paleobiology* 20:445–458.
- Gilinsky, N. L., and R. K. Bambach. 1987. Asymmetrical patterns of origination and extinction in higher taxa. *Paleobiology* 13:427–445.
- Gotelli, N. J., and G. R. Graves. 1996. *Null models in ecology*. Smithsonian Institution Press, Washington, D.C.
- Gradstein, F. M., J. G. Ogg, and A. G. Smith. 2004. *A geologic time scale 2004*. Cambridge University Press, Cambridge.
- Jablonski, D. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. *Science* 279:1327–1330.
- . 2001. Lessons from the past: evolutionary impacts of mass extinctions. *Proceedings of the National Academy of Sciences USA* 98:5393–5398.
- Jablonski, D., and G. Hunt. 2006. Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: organismic versus species-level explanations. *American Naturalist* 168:556–564.
- Jablonski, D., K. Roy, and J. W. Valentine. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* 314:102–106.
- Jin, J. 2001. Evolution and extinction of the North American *Hiscobeccus* brachiopod fauna during the Late Ordovician. *Canadian Journal of Earth Sciences* 38:143–151.
- Kowalewski, M., K. Gurs, J. H. Nebelsick, W. Oschmann, W. E. Piller, and A. P. Hoffmeister. 2002. Multivariate hierarchical analyses of Miocene mollusk assemblages of Europe: paleogeographic, paleoecological, and biostratigraphic implications. *Geological Society of America Bulletin* 114:239–256.
- Lande, R. 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13.
- Layou, K. M. 2007. A quantitative null model of additive diversity partitioning: examining the response of beta diversity to extinction. *Paleobiology* 33:116–124.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Miller, A. I. 1997. A new look at age and area: the geographic and environmental expansion of genera during the Ordovician radiation. *Paleobiology* 23:410–419.
- Miller, A. I., and S. Mao. 1998. Scales of diversification and the Ordovician radiation. Pp. 288–310 in M. L. McKinney and J. A. Drake, eds. *Biodiversity dynamics: turnover of populations, taxa, and communities*. Columbia University Press, New York.
- Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences USA* 98:5446–5451.
- Mussman, W. J., and J. F. Read. 1986. Sedimentology and development of a passive- to convergent-margin unconformity: Middle Ordovician Knox unconformity, Virginia Appalachians. *Geological Society of America Bulletin* 97:282–295.
- Okuda, T., T. Noda, T. Yamamoto, N. Ito, and M. Nakaoka. 2004. Latitudinal gradient of species diversity: multi-scale variability in rocky intertidal sessile assemblages along the Northwestern Pacific coast. *Population Ecology* 46:159–170.
- Patzkowsky, M. E. 1995. A hierarchical branching model of evolutionary radiations. *Paleobiology* 21:440–460.
- . 2007. Diversity partitioning of a Late Ordovician marine biotic invasion: controls on diversity in regional ecosystems. *Paleobiology* 33:295–309.
- R Core Development Team. 2006. *R: a language and environment for statistical computing*, Version 2.4.0. R Foundation for Statistical Computing, Vienna.
- Ruppert, E. E., and R. D. Barnes. 1994. *Invertebrate zoology*. Thomson-Brooks/Cole, Belmont, Calif.
- Scotese, C. R. 2001. *Atlas of earth history*, Vol. 1. Paleogeography. PALEOMAP Project, Arlington, Tex.
- Sepkoski, J. J., Jr. 1974. Quantified coefficients of association and measurement of similarity. *Mathematical Geology* 6:135–152.
- . 1981. A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology* 7:36–53.
- . 1988. Alpha, beta, or gamma: where did all the diversity go? *Paleobiology* 14:221–234.
- Sepkoski, J. J., R. K. Bambach, D. M. Raup, and J. W. Valentine. 1981. Phanerozoic marine diversity and the fossil record. *Nature* 293:435–437.
- Sepkoski, J. J., Jr., D. Jablonski, and M. Foote. 2002. A compendium of fossil marine animal genera. *Bulletins of American Paleontology* 363:1–560.
- Sheehan, P. M., and P. J. Coorough. 1990. Brachiopod zoogeography across the Ordovician-Silurian extinction event. In W. S. McKerrow and C. R. Scotese, eds. *Palaeozoic palaeogeography and biogeography*. Geological Society of London Memoir 12:181–187.
- Shen, S.-Z., and G. R. Shi. 2004. Capitanian (Late Guadalupian, Permian) global brachiopod palaeobiogeography and latitudinal diversity pattern. *Palaeogeography, Palaeoclimatology, Palaeoecology* 208:235–262.
- Stachowicz, J. J., R. B. Whitlatch, and R. W. Osman. 1999. Species diversity and invasion resistance in a marine ecosystem. *Science* 286:1577–1579.
- Stanley, S. M., and M. G. Powell. 2003. Depressed rates of origination and extinction during the late Paleozoic ice age: a new state for the global marine ecosystem. *Geology* 31:877–880.
- Veech, J. A., K. S. Summerville, T. O. Crist, and J. C. Gering. 2002. The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99:3–9.
- Whittaker, R. H. 1977. Evolution of species diversity in land communities. Pp. 1–67 in M. K. Hecht, W. C. Steere, and B. Wallace, eds. *Evolutionary biology*, Vol. 10. Plenum, New York.
- Wolda, H. 1981. Similarity indexes, sample-size and diversity. *Oecologia* 50:296–302.