

Origination, Extinction, and Dispersal: Integrative Models for Understanding Present-Day Diversity Gradients*

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ABSTRACT: Species diversity gradients seen today are, to a large degree, a product of history. Spatially nonrandom originations, extinctions, and changes in geographic distributions can create gradients in species and higher-taxon richness, but the relative roles of each of these processes remain poorly documented. Existing explanations of diversity gradients have tended to focus on either macroevolutionary or biogeographic processes; integrative models that include both are largely lacking. We used simple models that incorporate origination and extinction rates along with dispersal of taxa between regions to show that dispersal not only affects regional richness patterns but also has a strong influence on the average age of taxa present in a region. Failure to take into account the effects of dispersal can, in principle, lead to biased estimates of diversification rates and potentially wrong conclusions regarding processes driving latitudinal and other gradients in diversity. Thus, it is critical to include the effects of dispersal when formulating and testing hypotheses about the causes of large-scale gradients in diversity. Finally, the model results, in conjunction with the results of existing empirical studies, suggest that the nature of macroevolutionary and biogeographic processes may differ between terrestrial and marine diversity gradients.

Keywords: diversity gradient, origination, extinction, dispersal, biogeography, models.

With human footprints covering every habitat on the planet and the resulting threats to biodiversity, the need to understand the processes that determine why some regions have many species while others have relatively few has never been greater. Yet despite many hypotheses and a considerable literature, we still know relatively little about what causes large-scale gradients in diversity (Currie et al. 2004; Mittelbach et al. 2007). Recent work has fo-

cused largely on the role of the present-day environment in regulating regional diversity, and while such analyses have revealed much about the diversity-environment relationship, process-based explanations of these patterns remain elusive (Currie et al. 2004). Climate clearly has an influence on large-scale patterns of species diversity, and numerous studies have demonstrated strong correlations between diversity and present-day environmental variables such as temperature and productivity (e.g., Currie 1991; Roy et al. 1998; Mittelbach et al. 2001; Hawkins et al. 2003; Currie et al. 2004). But as Ricklefs (2004) pointed out, it is not straightforward to interpret these correlations or to demonstrate that they reflect causality. Present-day environmental variables could regulate spatial patterns of species diversity by influencing geographic range limits of individual species, the carrying capacity of a particular place, or both (Allen et al. 2002; Currie et al. 2004). Thus, one possible explanation of the correlations between present-day climatic variables and diversity gradients is that the latter simply reflect how environmental conditions influence spatial patterns of species distributions or how they constrain interactions between species that determine local coexistence. Under this view, historical factors such as speciation and extinction either do not show strong spatial biases or are secondary. Alternatively, the correlations between present-day climate and diversity may predominantly reflect a historical signal of speciation and extinction, along with phylogenetic conservatism of ecological, life-history, and physiological traits (Ricklefs 2004, 2006a; Wiens and Donoghue 2004). Note that in the latter scenario, climate can still have a role in regulating diversity patterns through its influence on speciation and extinction, but the emphasis is shifted to the roles of past environments as well as other factors, such as biotic interactions, that promote speciation and extinction (Schemske 2002). In general, present-day diversity gradients reflect the influences of spatially nonrandom originations and extinctions as well as changes in the geographic distributions of taxa over time (see Jablonski et al. 2006). The challenge, then, is to untangle the relative roles of macroevolutionary dynamics and biogeographic processes.

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Here we build on some recent studies and use integrative models that incorporate dispersal between regions, along with spatially variable origination and extinction rates, to explore how dispersal affects the nature of diversity gradients. In particular, we ask whether ignoring dispersal dynamics is likely to affect our estimates of macroevolutionary rates and our ability to separate the relative contributions of macroevolutionary and biogeographic dynamics in generating diversity gradients. We address this issue in the context of the latitudinal diversity gradient primarily because of the large body of work associated with that gradient, but the general results presented here should be applicable to other gradients, such as those along longitude, bathymetry, and elevation. We also use these models to explore whether latitudinal diversity gradients in marine and terrestrial systems are likely to result from different dynamics.

Untangling Patterns and Processes

Existing attempts to understand the causes of the latitudinal diversity gradient have focused either on the roles of current environmental variables (e.g., Currie 1991; Roy et al. 1998; Mittelbach et al. 2001; Hawkins et al. 2003; Currie et al. 2004) or on geographic patterns of origination, extinction, and diversification (see Jablonski et al. 2006). Except for a few studies (e.g., Hawkins et al. 2005; Harrison et al. 2006; Jablonski et al. 2006; Wiens et al. 2006), integrative analyses of diversity gradients that include macroevolutionary as well as biogeographic and ecological processes are largely lacking. This makes it difficult, if not impossible, to evaluate the relative roles of these processes in shaping present-day diversity gradients.

The idea that contemporary climate plays an important role in determining global diversity gradients goes back almost two centuries (Clarke and Gaston 2006). However, there are still very few process-based models relating past or present environmental conditions to large-scale patterns of species diversity, and hence quantitative predictions about diversity-environment or diversity-energy relationships are lacking (Rosenzweig 1995). Support for a strong influence of the present-day environment on diversity gradients is almost exclusively based on significant positive relationships between measurements of various climatic or environmental variables (e.g., temperature, productivity, water availability) and species or higher-taxon richness (see Currie et al. 2004 for a review). But the slopes of these regressions vary widely across taxa and/or regions, and the empirical data are largely inconsistent with the commonly cited explanations of such relationships (Currie et al. 2004). In cases where specific predictions about the slopes of relationships are available, such as the link between diversity and temperature predicted by Allen et al.

(2002), results of empirical tests have been mixed (Allen et al. 2002; Roy et al. 2004; Hunt et al. 2005). Some authors have even argued that a general species-energy relationship that applies to both plants and animals is unlikely to exist and that the effect of temperature on diversity is likely to be indirect and complex (Clarke and Gaston 2006; also see Currie et al. 2004). Thus it is not straightforward to interpret the observed correlations between contemporary environmental variables and diversity and to demonstrate that they reflect causality (see Ricklefs 2004).

The hypothesis that present-day diversity gradients bear a strong imprint of history is also not new. Wallace (1878) was among the first to argue that parts of the world with a longer and more stable geological and climatic history have had a chance to accumulate more species compared to areas, such as high latitudes, that have seen large environmental fluctuations in the geological past. This general idea, in various forms, has had proponents ever since, as have other macroevolutionary hypotheses about the origin and maintenance of the latitudinal diversity gradient (Jablonski et al. 2006; Mittelbach et al. 2007). However, most analyses of historical influences on the present-day latitudinal diversity gradient have focused on how origination and/or diversification rates vary with latitude (patterns of extinction remain poorly known) and have ignored the effects of postorigination changes in the distribution of taxa (Jablonski et al. 2006). Yet large-scale gradients in species richness today almost certainly reflect the interactions between how originations and extinctions vary in space and changes in geographic distributions of taxa in response to changes in the ambient environment (Wiens and Donoghue 2004; Jablonski et al. 2006; Ricklefs 2006a). Equally important, even though there is increasing recognition that history can be an important determinant of present-day diversity gradients, the effects of historical processes are still studied largely using descriptive and retrospective analyses rather than tests of specific models incorporating speciation, extinction, and dispersal dynamics (but see Goldberg et al. 2005; Jablonski et al. 2006; Wiens et al. 2006).

We argue that the first step toward a better understanding of the processes underlying the contemporary latitudinal diversity gradient should be to evaluate the relative roles of macroevolutionary dynamics (i.e., origination and extinction) and biogeographic dynamics (i.e., patterns of immigration, local extinctions, and distributions of geographic range limits) using general models that relate spatial patterns of speciation, extinction, and changes in geographic distributions of individual taxa to large-scale gradients in diversity. Understanding the relative contributions of macroevolutionary and biogeographic or paleobiogeographic dynamics in determining the present-day latitudinal diversity gradient would allow us to focus better

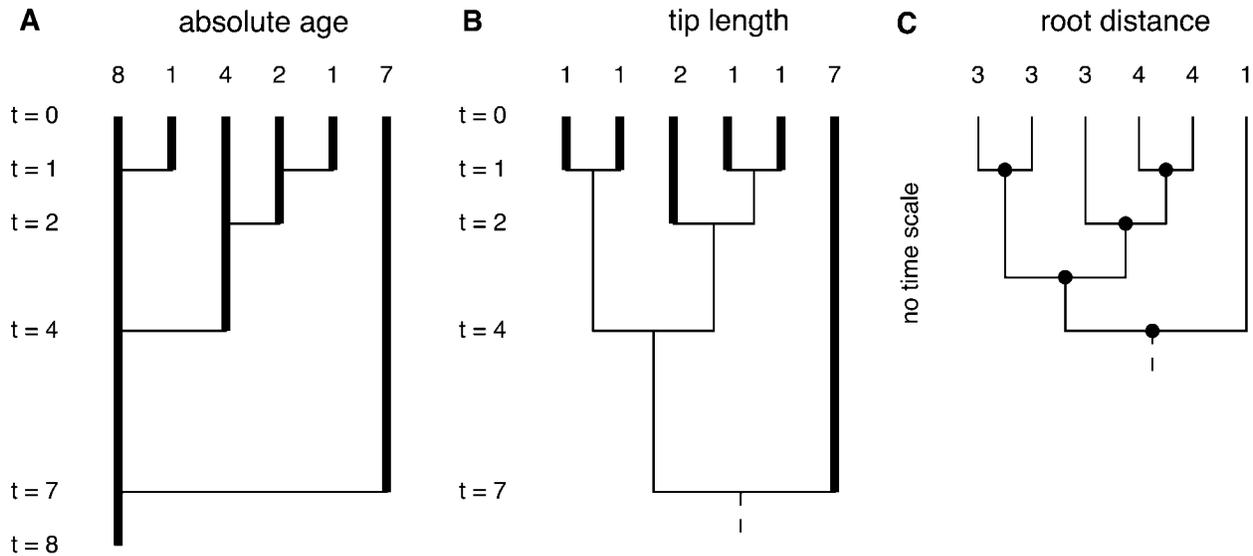


Figure 1: Illustrations of the three age metrics on a simple hypothetical tree. The number above each tip denotes the age of that taxon. *A*, Absolute age is the duration from the present time to the time of origination of a lineage. A good fossil record is required to obtain the time of origination. The absolute age of a taxon is not affected by origination or extinction events of other taxa, so sister taxa can have different absolute ages. *B*, Tip length is the duration from the present time to the most recent node (i.e., origination event that appears in the reconstructed phylogeny) of the lineage. Tip lengths (and lengths of internal branches) can be obtained from molecular phylogenies, but the length of any one branch can be affected by origination and extinction of other taxa. *C*, Root distance is simply the number of nodes between a tip and the root of a tree. Shorter tip lengths generally (but not perfectly) correspond to greater root distances. Note that the tree representations used for these metrics, from left to right, contain decreasing amounts of information.

on potential mechanisms that are likely to be important. It would also allow us to explore whether the contemporary latitudinal diversity gradient in some groups largely reflects macroevolutionary processes (i.e., differential originations and/or extinctions) while in others is more a function of how past and present environments influence biogeographic dynamics. Historical processes are often somewhat idiosyncratic and have therefore been deemed essentially untestable by some authors (Francis and Currie 1998), but model-based approaches can form the basis for developing a general framework for analyzing their role in producing diversity gradients.

Models of Diversity Gradients

The models discussed here are special cases of the two-region model of Goldberg et al. (2005). These dynamic models track the number of taxa and their ages in each of two regions, R_a and R_b , over time. The regions can have different per taxon rates of origination (s_a and s_b), extinction (x_a and x_b), and dispersal or range expansion (d_a from R_a to R_b and d_b from R_b to R_a). These rates are assumed to be constant over time and across taxa, and the macroevolutionary process is modeled as a multistate branching process. For taxa present in both regions at any

particular time, extinctions in each region are independent events and represent range contractions (i.e., they are local extinctions); for taxa present in only one region, extinctions are global. In each model used here, we chose R_a to be the region of greater expected richness. Using this framework, we explored the relationship between taxon richness and the average age of taxa in each of the two regions under different scenarios of origination, extinction, and dispersal. We focused on taxon ages because they are widely used for calculating diversification rates using molecular phylogenies (Nee et al. 1994; Gaston and Blackburn 1996; Magallón and Sanderson 2001; Cardillo et al. 2005; Nee 2006; Ricklefs 2006*b*; Weir and Schluter 2007) or data from the fossil record (Flessa and Jablonski 1996; Foote 2001; Goldberg et al. 2005; Allen et al. 2006; Jablonski et al. 2006).

For each model described below we calculated average ages, a commonly used metric (e.g., Gaston and Blackburn 1996; Weir and Schluter 2007), using three different approaches (fig. 1). First, we used absolute ages of taxa, such as those derived from the fossil record, where the age of a lineage is simply its first stratigraphic occurrence. Next, we used tip lengths, as would be obtained from a molecular phylogeny, where the most recent branching point of a lineage depends on the time of an origination event and

on the survival of its sister taxon (see Chown and Gaston 2000). Finally, we used root distance, obtained by counting the number of nodes between each tip and the root of a phylogenetic tree; this metric has been used in lieu of tip length when branch lengths are not available on a phylogeny (Kerr and Currie 1999; Hawkins et al. 2006). For all the models presented below, tip lengths and root distances yielded qualitatively similar results, so we only show the results for the absolute ages and tip lengths.

For each set of parameter values, determined by the models described below, we calculated the proportional difference in richness between the regions, $(R_a \text{ richness} - R_b \text{ richness}) / (R_a \text{ richness} + R_b \text{ richness})$, and the difference in average age, as measured by each metric. Because R_a is always the more diverse region, the proportional richness difference varies between 0 (when R_a and R_b have equal numbers of species) and 1 (when R_b has no species). It does not, however, vary linearly with the ratio of R_b richness to R_a richness; when R_b has half as many species as R_a , the proportional richness difference is one-third. These calculations were based on a continuous-time branching process in which origination, extinction, and dispersal proceed under the assumptions of the two-region model. The initial condition of this process was taken to be a single lineage present in both regions, and the process was run for 10 time units. In some cases this did not provide sufficient time for the relative proportions of taxa in each geographic region to reach equilibrium, but fixing the time elapsed seems more analogous to the empirical situations we are trying to model than insisting on effectively infinite intervals. For the absolute-age metric, richness and average age were calculated analytically following the methods of Goldberg et al. (2005). For the tip length and root distance metrics, analytical solutions are not available, so we calculated richness and average age differences for each of 10,000 simulated trees and then averaged the results. Note that all simulated trees used here are global phylogenies (i.e., they include species in both regions).

Each of the models described below (and summarized in table 1) was designed to represent an existing hypothesis about the causes of the present-day latitudinal diversity gradient, and in "Discussion" we have attempted to relate the insights derived from these models to results of previous empirical studies. The primary difference between

these models and most previous work is that here, in each case, we evaluated the effects of origination and extinction in conjunction with dispersal rather than separately looking at evolutionary and biogeographic processes.

Model 1: pure dispersal model. If shifts in geographic range limits due to changes in the environment are the main driver of diversity gradients, then such gradients should result from preferential movement of taxa into regions that can support more species and not from spatial gradients in macroevolutionary rates. Such high-diversity areas could represent those that have higher energy (e.g., the species-energy hypothesis; Currie 1991) or some other attribute of the environment allowing many taxa to coexist (e.g., Allen et al. 2002). From a macroevolutionary perspective, this is the null hypothesis, where diversification rates do not show a spatial bias (Ricklefs 2006b). In fact, the implicit assumption of most regression studies relating diversity gradients to gradients in present-day environmental variables (see Currie et al. 2004 for a review), as well as some null models used in analyses of diversity gradients (Colwell and Lees 2000; Jetz and Rahbek 2002; Storch et al. 2006), is that originations and extinctions are not spatially biased. In the model used here, R_a and R_b have identical origination and extinction rates ($s_a = s_b$, $x_a = x_b$), but after origination, species are much more likely to disperse into R_a than R_b ($d_a \ll d_b$). Thus the diversity gradient, in this case, should result not from differences in evolutionary rates between R_a and R_b but solely from higher dispersal of taxa into R_a .

Model 2: macroevolutionary source-sink model. Biogeographers have long postulated that certain regions of the world represent centers of origin—areas where species and higher taxa preferentially originate—and that these areas are generally situated in lower latitudes (see Ricklefs and Schluter 1993; Brown and Lomolino 1998). Over time, taxa spread outward from these centers of origin into regions with much lower origination rates, or macroevolutionary sinks (Goldberg et al. 2005). Thus, the rate of spread and the difference in origination rates between the regions determine the strength of the diversity gradient. In the case of a pure source-sink system there would be no originations in the sink, but in reality this extreme is unlikely. Under our model, a source-sink system has $s_a \gg s_b$, $x_a = x_b$, and $d_a \gg d_b$. Note that this characteri-

Table 1: Summary of the parameters used in each model

Model	Name	Origination	Extinction	Dispersal
1	Pure dispersal	$s_a = s_b$	$x_a = x_b$	$d_a \ll d_b$
2	Macroevolutionary source-sink	$s_a \gg s_b$	$x_a = x_b$	$d_a \gg d_b$
3	Out-of-the-tropics	$s_a \gg s_b$	$x_a \ll x_b$	$d_a \gg d_b$
4	Wallace	$s_a = s_b$	$x_a \ll x_b$	$d_a \gg d_b$ or $d_a = d_b$

zation of a macroevolutionary sink follows Goldberg et al. (2005) but is somewhat different from a demographic sink, in which the death rate is high (e.g., Pulliam 1988).

Model 3: out-of-the-tropics model. Analyses using taxon ages derived from the fossil record (Flessa and Jablonski 1996; Goldberg et al. 2005), paleontological data on the time and place of origin of individual taxa (Jablonski 1993; Jablonski et al. 2006), and phylogenetic relationships of taxa (Judd et al. 1994; McKenna and Farrell 2006) all suggest that the latitudinal diversity gradient results from taxa preferentially originating in lower latitudes, persisting there over geological time, and expanding their geographic distributions into high latitudes. This dynamic of tropical origination followed by expansion into higher latitudes, called the out-of-the-tropics (OTT) model (Jablonski et al. 2006; also see Ricklefs 2006a), is a variant of the source-sink model with a much lower extinction rate in the source region. In our case, this means $s_a \gg s_b$, $x_a \ll x_b$, and $d_a \gg d_b$.

Model 4: Wallace model. Wallace (1878) was among the first to argue that present-day diversity gradients bear a legacy of past changes in climate. This general idea, in various forms, has had proponents ever since (see Jablonski et al. 2006; Weir and Schluter 2007) and postulates that parts of the world with a longer and more stable geological and climatic history have had a chance to accumulate more species than areas such as high latitudes that have seen large environmental fluctuations (and hence higher extinctions) in the geological past. Thus, in this case, the main driver of the diversity gradient is higher extinction in the region with fewer species. In terms of dispersal, empirical tests of this hypothesis done at the level of clades and higher taxa argue that the gradient is partially driven by dispersal of taxa from low to high latitudes (i.e., from the regions that are more stable to those rebounding from extinctions; e.g., Hawkins et al. 2006). Others focusing on species-level gradients highlight the importance of differential speciation and extinction rather than dispersal (e.g., Weir and Schluter 2007). We therefore modeled this hypothesis in two different ways to reflect these views: first, we assumed dispersal to be much greater from the region with low extinction to the one with high extinction (i.e., from low to high latitudes), and second, we assumed dispersal to be equal in both directions. In our model, this translates to $s_a = s_b$, $x_a \ll x_b$, and either $d_a \gg d_b$ or $d_a = d_b$. The main conceptual difference between the OTT model and the Wallace model is that in the former, origination is higher in low latitudes, while in the latter, it is the same across latitudes.

Results

The results of all the models clearly show that the average age of the lineages present in a region depends not only

on origination and extinction rates but also on the magnitude and direction of dispersal. Of the four models considered here (summarized in table 1), perhaps the most surprising result comes from the pure dispersal model (model 1), the null model in terms of macroevolutionary rates. In this case, dispersal into one region (R_a) not only creates a difference in diversity between the two regions but also affects the average age of taxa in each region. Thus, greater dispersal into R_a leads to greater differences in taxon richness and in average age between the regions even though the actual diversification rates do not differ (fig. 2). Moreover, the sign of the difference in average age (and, to a smaller extent, its magnitude) depends on whether we use absolute ages of taxa, such as those derived from the fossil record, or tip lengths, as estimated from a phylogeny. For absolute ages, the more diverse region (R_a) has the younger average age (fig. 2A), but for tip lengths, the less diverse region has the younger average age (fig. 2B).

To understand the observed differences between the regions and why the two metrics behave so differently, it is useful to consider a single tree generated under this model with the added simplification of no extinction (i.e., a pure birth model; fig. 3). The higher richness in R_a not only results from direct immigration but also is magnified by the origination of descendants from those immigrants; descendants in R_b may become immigrants themselves, but descendants in R_a remain endemic to R_a . As for the average ages, when dispersal is high, there are few R_b endemics (because these rapidly become cosmopolitans, i.e., present in both regions) and many R_a endemics (because these arise from both R_a endemics and cosmopolitans). The average age of R_b taxa is, therefore, largely determined by cosmopolitans and that of R_a taxa by R_a endemics. With the absolute-age metric, cosmopolitan lineages are older, on average, than R_a endemics because sufficient time must have elapsed not only for their origination but also for their dispersal; R_a taxa are thus younger on average than R_b taxa. For the tip length metric, on the other hand, cosmopolitan lineages are younger, on average, than R_a endemics because the time to the most recent branching point in the reconstructed phylogeny is inversely related to the effective speciation rate. Cosmopolitan lineages have a higher effective origination rate because they can speciate in either region, while R_a endemics can speciate only in R_a . Cosmopolitan lineages are therefore younger, making the average for R_a older than that for R_b . Adding extinction (as in fig. 2) decreases the age difference between the regions under the absolute-age metric but increases it under the tip length metric. This is because extinction decreases expected absolute ages but increases expected tip lengths (Chown and Gaston 2000), and the effective global

Model 1: pure dispersal

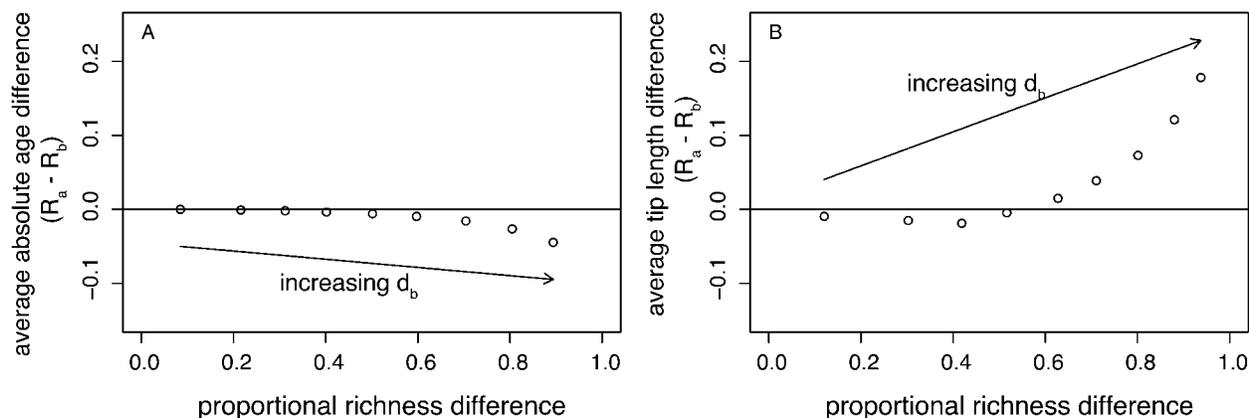


Figure 2: Differences in average age between the two regions (R_a and R_b) under model 1, the pure dispersal model. The X-axis shows the proportional difference in taxon richness ($(R_a \text{ richness} - R_b \text{ richness}) / (R_a \text{ richness} + R_b \text{ richness})$); R_a is always the more diverse region, so x values can range from 0 to 1. The Y-axis shows the difference in age between the regions (R_a average age $- R_b$ average age); when this is positive, R_a is older, and when it is negative, R_a is younger. *A*, Age differences using the absolute-age metric; *B*, age differences using the tip length metric (see fig. 1). Parameter values for all points are $s_a = s_b = 1.0$, $x_a = x_b = 0.5$, $d_a = 1 \times 10^{-6}$. In each panel, from left to right, the points show values for $d_b = 0.02, 0.06, 0.10, 0.15, 0.23, 0.35, 0.60, 1.20, 4.00$; these values were chosen for roughly equal spacing in proportional richness difference. With either age metric, higher dispersal causes large diversity differences and moderate average age differences between the regions, but the two age metrics give age differences of opposite sign (see fig. 3 and text for explanation).

extinction rate is lower for cosmopolitans than for endemics.

For the macroevolutionary source-sink model (model 2), the results shown here are consistent with those of Goldberg et al. (2005). In this model, the sink region (R_b) serves as a region of accumulation of older taxa, since older lineages have a greater time-integrated probability of dispersal, and hence R_b has an older average age than the source region (R_a ; fig. 4). Larger per capita dispersal rates increase the probability of younger taxa dispersing from R_a to R_b , thereby reducing the difference in average age, but the sink can never be younger than the source. Similarly, the difference in diversity between the two regions also depends on the rate of dispersal; when dispersal is high, it is possible for the two regions to have similar levels of diversity even though the underlying diversification rates are very different. Note that unlike in model 1, the results are qualitatively the same whether one uses absolute ages (fig. 4A) or tip lengths (fig. 4B).

Our exploration of the OTT model (model 3) of Jablonski et al. (2006) reveals that when taxa preferentially originate in region R_a and expand their distributions to R_b , R_a always has a younger average age than R_b (fig. 5). The magnitude of the difference in average ages decreases with increasing dispersal into R_b or increasing extinction in R_b . These results are similar to those of model 2 because the OTT model is a variant of the source-sink model, and

they are consistent with the findings of previous empirical analyses (Goldberg et al. 2005; Jablonski et al. 2006). However, our results also show that when extinction is very high in the recipient region (large x_b) or dispersal from R_a to R_b is rapid (large d_a), it is possible for the regional differences in average age or diversity to virtually disappear even though the OTT dynamic still operates (fig. 5). Thus, once again, dispersal may cause the two regions to look very similar even when they differ greatly in diversification rates. The qualitative results in this case are the same whether we use absolute ages (fig. 5A) or tip lengths (fig. 5B).

Of our four models, the Wallace model (model 4) is the only one where the gradient in diversity is driven primarily by the difference in extinction rates between the two regions. In this case, the average age is generally younger in R_b , the region with higher extinction and lower diversity (fig. 6). While this result is intuitively obvious, what is interesting is that under such a scenario, where origination rates do not differ between the regions, the age difference is relatively insensitive to dispersal—there are only small differences between results from balanced dispersal between the two regions and those from preferential dispersal from R_a to R_b . The maximum difference is observed at moderate extinction rates in R_b ; as x_b increases, surviving lineages in R_b get younger, but when extinction in R_b exceeds origination there, immigrant lin-

Model 2: source–sink

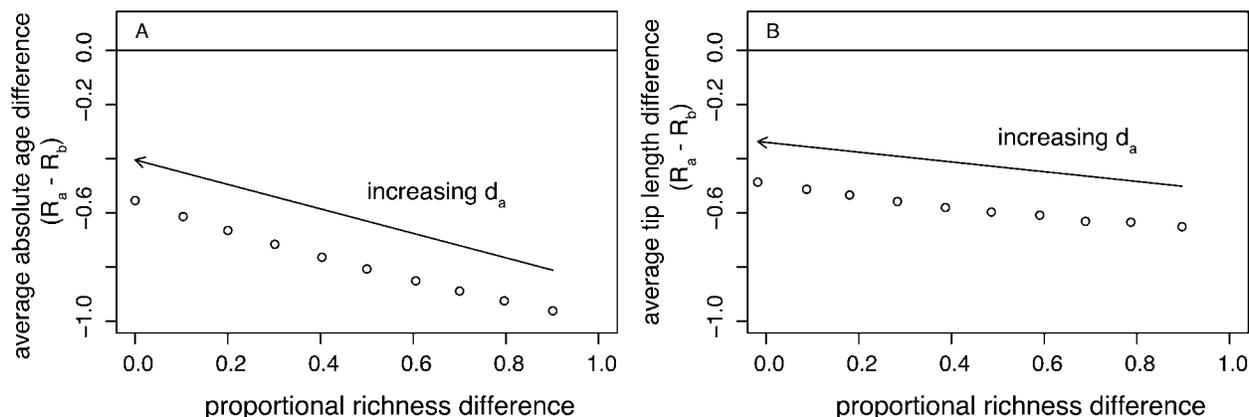


Figure 4: Differences in average age between the two regions under model 2, the source-sink model. Axes and panel layout are the same as in figure 2. Parameter values are $s_a = 1.0$, $s_b = 1 \times 10^{-6}$, $x_a = x_b = 0.5$, $d_b = 1 \times 10^{-6}$, $d_a = 3.00, 2.05, 1.50, 1.10, 0.81, 0.60, 0.42, 0.29, 0.18, 0.08$. In this case, both age metrics show similar behavior. The more diverse source region (R_a) is always younger than the sink region (R_b), although the diversity and age differences decrease with larger dispersal rates.

ages, which tend to be older, contribute relatively more to richness in R_b . Again, the qualitative results hold irrespective of which age estimate we use (fig. 6A, 6B).

Discussion

Why We Should Not Ignore Dispersal

The model results shown above reveal not only that dispersal influences the steepness (i.e., relative difference in richness) of diversity gradients but also that movement of taxa between regions can affect our ability to estimate regional origination and extinction rates retroactively. Thus, they once again underscore the need to consider the effects of dispersal, in conjunction with origination and extinction, in order to understand the processes that shape spatial patterns of diversity. Our results are consistent with those of previous empirical analyses that have demonstrated a strong influence of postorigination changes in taxon distributions on the strength of the latitudinal diversity gradient (Goldberg et al. 2005; Jablonski et al. 2006; Wiens et al. 2006), but they also show that failure to include dispersal effects while testing various hypotheses about the drivers of the latitudinal diversity gradient can lead to wrong conclusions.

The clearest example of this comes from model 1, where two regions with identical origination and extinction rates show a difference in diversity and average age simply due to asymmetric dispersal from one region to another (fig. 2). Thus, in this case, retroactive calculations of evolutionary rates based on species richness and taxon age (e.g.,

using lineage-through-time plots or other methods that rely on ages of living taxa) could lend support to the hypothesis that the difference in diversity is a direct result of differences in diversification rates between the two regions even though in reality the per capita origination and extinction rates are exactly the same. The situation is further complicated by the fact that which region is younger could depend on the age metric used. As shown in figure 2, if we use the average ages of regions to test whether the region with higher diversity is a cradle or a museum in a macroevolutionary sense (e.g., Gaston and Blackburn 1996), we would conclude that region R_a is a cradle (sensu Stebbins 1974; see Jablonski et al. 2006) based on paleontological data (fig. 2A) but a museum based on ages derived from molecular phylogenies (fig. 2B). Obviously neither is true, given the real model. Conversely, as seen in the out-of-the-tropics model, it is possible for the average ages of two regions or their diversities not to differ substantially even when the origination rate is considerably higher in one than in the other (fig. 5).

The effect of dispersal on regional differences in average age is greater under some models than under others, but whether it is measurable in real-world data would depend on the true parameter values, the time resolution of the data set, and the importance of any other confounding processes that may be acting. We are therefore certainly not claiming that all previous empirical tests of hypotheses about the latitudinal diversity gradient using taxon ages but without taking into account the effects of dispersal have reached wrong conclusions regarding macroevolutionary dynamics. But our results clearly show that, in

Model 3: out of the tropics

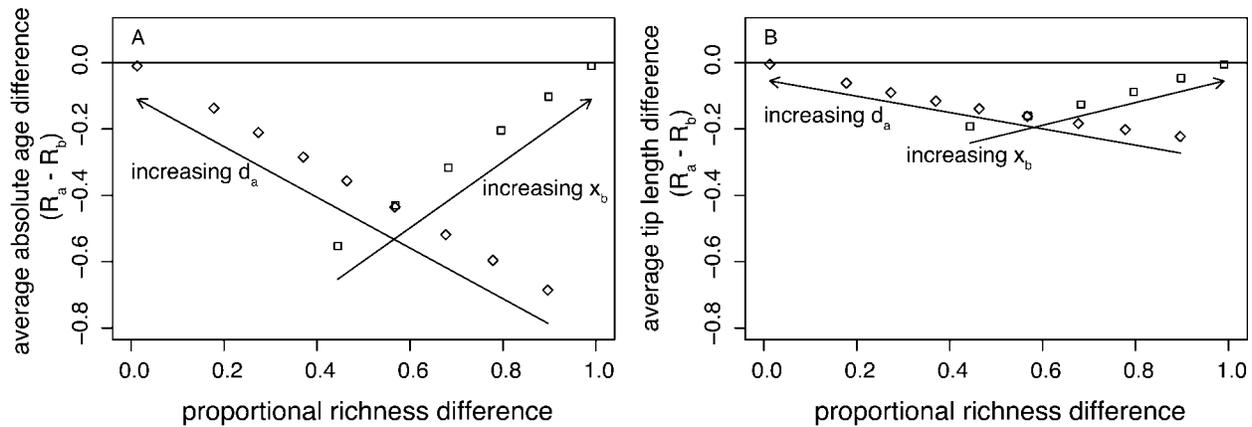


Figure 5: Differences in average age between the two regions under model 3, the out-of-the-tropics model. Axes and panel layout are the same as in figure 2. Parameter values are $s_a = 0.8$, $s_b = x_a = d_b = 1 \times 10^{-6}$. For the squares, $d_a = 1.00$, $x_b = 0.001, 0.52, 1.35, 3.10, 8.00, 100$; for the diamonds, $x_b = 0.5$, $d_a = 100, 6.00, 3.45, 1.50, 0.99, 0.62, 0.37, 0.15$. The two age metrics show similar behavior in this case. As in model 2 (fig. 4), the more diverse region is always younger, although diversity and age differences decrease with larger dispersal rates. Greater extinction in the recipient region increases the diversity difference and decreases the age difference because recent immigrants are younger and are more likely to survive there.

principle, dispersal by itself can lead to biased estimates of diversification rates and hence to potentially wrong conclusions about underlying processes. This issue is analogous to the biases that occur when estimating rates of character change without accounting for character-dependent diversification (Maddison 2006). Also, because of these complex interactions between origination, extinction, and dispersal and, potentially, the types of age estimates used, we strongly caution against using qualitative predictions about how taxon ages (or evolutionary rate estimates based on such ages) would vary among regions when testing hypotheses about the macroevolutionary dynamics underlying diversity gradients (e.g., Stevens 2006).

To avoid misinterpretations, it is essential to analyze real data using models that account for all three processes rather than separately testing macroevolutionary and biogeographic dynamics, as is currently the norm (but see Xiang et al. 2004; Goldberg et al. 2005; Hawkins et al. 2006; Jablonski et al. 2006; Wiens et al. 2006). Analyses that explicitly account for the effects of dispersal either using direct evidence (Jablonski et al. 2006) or through model fitting (Goldberg et al. 2005; Wiens et al. 2006) can separate the contributions of ecological and evolutionary processes in generating spatial gradients in diversity. This approach also allows us to focus better on the actual mechanisms that produce diversity gradients. For example, climate can affect diversity gradients either through its influence on originations and extinctions or through its effects on dispersal and the geographic distributions of

taxa. Obviously the actual mechanisms involved in each case are different, and the relative importance of each depends on whether the diversity gradient seen in a clade is primarily due to differences in macroevolutionary rates or to biogeographic processes such as dispersal of taxa from one region to another.

Since our focus in this article is on general models of diversity gradients that integrate macroevolutionary and biogeographic dynamics, we assume that all six rates in our models are stochastically constant over time. While this is a widely used approach in macroevolutionary analyses, it does not allow us to explore the effects of time-dependent changes in origination, extinction, and dispersal or the effects of phylogenetic selectivities in any of these parameters. Some existing hypotheses about the latitudinal diversity gradient (e.g., the niche conservatism hypothesis of Wiens and Donoghue [2004]) invoke nonrandom extinctions and dispersals (Hawkins et al. 2006; Wiens et al. 2006), and we certainly do not deny that such processes may play important roles in determining regional diversity levels. However, evaluating such nonneutral or time-dependent hypotheses requires tests beyond simply comparing average differences in ages or rates. Modeling these more complex dynamics would require specific information about the nature, timing, and magnitude of the changes as well as phylogenetic conservatism of ecological and physiological traits, information currently unavailable for most taxa. In addition, those specifics are likely to vary from one clade to another and between different regions. Our results are, therefore, best

Model 4: Wallace hypothesis

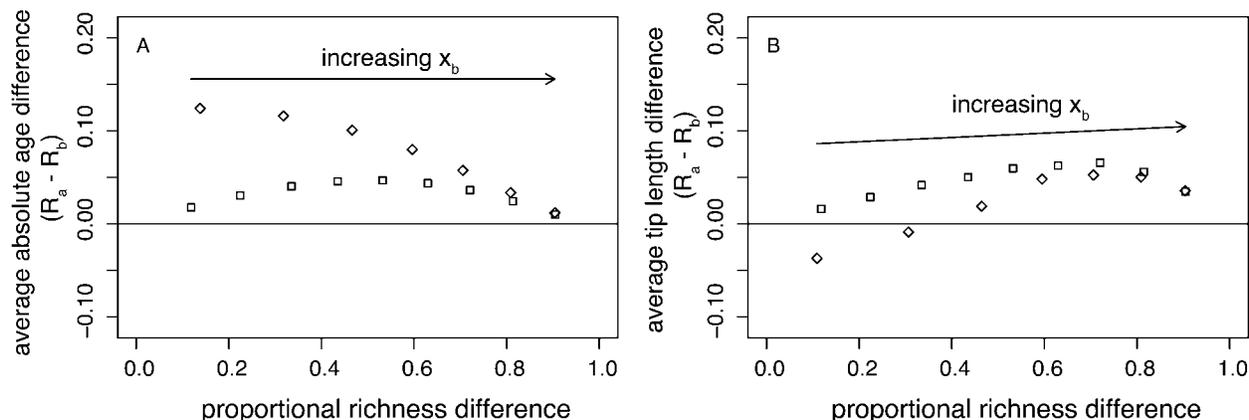


Figure 6: Differences in average age between the two regions under model 4, the Wallace hypothesis model. Axes and panel layout are the same as in figure 2. Parameter values are $s_a = s_b = 0.6$, $x_a = 1 \times 10^{-6}$, $d_a = 0.5$. For the squares, $d_b = 0.5$, $x_b = 0.13, 0.26, 0.42, 0.60, 0.83, 1.16, 1.65, 2.60, 5.25$; for the diamonds, $d_b = 1 \times 10^{-6}$, $x_b = 0.42, 0.60, 0.83, 1.16, 1.65, 2.60, 5.25$. The age metrics show slightly different behavior, but for both, species are generally younger in the less diverse region. The magnitude of the age difference is relatively insensitive to the amount of extinction in region b (R_b) or dispersal from region a (R_a) to R_b .

viewed as quantitative explorations of general and long-standing ideas about the processes structuring diversity gradients, where the neutral assumption is helpful and widely used in empirical analyses (e.g., Flessa and Jablonski 1996; Gaston and Blackburn 1996; Cardillo et al. 2005; Ricklefs 2006b; Weir and Schluter 2007).

*Are Marine and Terrestrial Diversity Gradients
Driven by Different Processes?*

A number of studies have quantified how macroevolutionary rates of taxa vary along latitude, and although the results are difficult to compare directly, given the variety of methods and types of data used (see Jablonski et al. 2006), they reveal a potentially interesting difference between marine and terrestrial clades. For marine mollusks, paleontological data show that taxa not only preferentially originate in lower latitudes but also tend to persist there over geological time while spreading to higher latitudes (Jablonski 1993; Flessa and Jablonski 1996; Crame 2002; Goldberg et al. 2005; Jablonski et al. 2006). This dynamic, combined with higher extinctions in high latitudes, leads to a latitudinal gradient in diversity (Crame 2002; Jablonski et al. 2006). Under this hypothesis, the out-of-the-tropics model of Jablonski et al. (2006), high latitudes represent a macroevolutionary sink and average ages of taxa should increase with latitude (Goldberg et al. 2005; also see fig. 5A). In contrast to analyses of marine mollusks, analyses of age distributions of avian taxa, derived from molecular phylogenies, have painted a somewhat different

picture, with high latitudes harboring more recently derived and hence younger species and clades of birds compared to those found in the tropics (Hawkins et al. 2006; Weir and Schluter 2007). This shift toward younger taxa in extratropical latitudes is interesting, given that diversification rates of birds appear to be higher in low latitudes (Cardillo et al. 2005; Hawkins et al. 2006; Ricklefs 2006b; Weir and Schluter 2007), although whether this is due to higher origination or lower extinction rates remains unclear (Ricklefs 2006b). A recent study of North American birds provides evidence that speciation and extinction rates increase with latitude (Weir and Schluter 2007), while other, more global analyses of bird clades suggest potentially higher origination rates in low latitudes (Hawkins et al. 2006; Ricklefs 2006b).

Since diversity gradients in all taxa, including birds and mollusks, are driven by interactions between the three processes in our models, the first step toward understanding why latitudinal patterns of taxon ages differ in the two groups would be simply to ask under what combinations of origination, extinction, and dispersal would one expect high-latitude, low-diversity assemblages to be younger than low-latitude, high-diversity assemblages. Of the models presented here, the source-sink, out-of-the-tropics, and Wallace models (models 2–4) all invoke higher diversification rates in one region (R_a) than in the other (R_b), analogous to the tropical-extratropical case. Of these three, the only model that can yield a younger average age in the low-diversity region (R_b) is the Wallace model, where the origination rates are similar in the two regions (fig.

6). Neither the source-sink model nor the OTT model, both with higher origination rates in the source region, mimics the empirical trend seen in New World birds where temperate latitudes are enriched in younger clades and species compared to the tropics (Hawkins et al. 2006; Weir and Schluter 2007). In the OTT model, increasing dispersal or the extinction rate in the region with the lower diversification rate makes the average ages of the two regions more similar, but it cannot make the lower-diversity region younger (fig. 5). Unlike in the pure dispersal model (model 1), the qualitative results in these cases do not change whether one uses absolute- or relative-age estimates (figs. 4–6), so the observed difference between birds and marine mollusks is unlikely to be due to the use of phylogenetic age estimates for birds and fossil-based absolute ages for marine mollusks.

In combination, these results suggest that for birds, the observed latitudinal difference in taxon ages and/or diversification rates reflects either (1) higher extinction in the extratropical regions rather than higher origination in lower latitudes (Weir and Schluter 2007) or (2) time-inhomogeneous processes, including selective extinctions and dispersal of taxa into the extratropics (Hawkins et al. 2006). In either case, the situation appears to be different from that in marine mollusks, where the hypothesis of a latitudinal gradient in origination rates is supported by analyses of taxon age distributions using time-homogeneous models, such as those discussed here (Goldberg et al. 2005), or direct evidence from the fossil record (Jablonski 1993; Jablonski et al. 2006). Furthermore, in marine mollusks, most taxa show preferential origination in the tropics followed by the expansion of geographic ranges into high latitudes (Goldberg et al. 2005; Jablonski et al. 2006), while in birds, such northward expansion of geographic ranges apparently involves only select clades (Hawkins et al. 2006). In fact, the current data are even consistent with the possibility that the latitudinal gradient in diversification rates in birds, at least at the species level, is driven solely by high extinctions in temperate and polar regions, with no latitudinal difference in origination rates and no spatial bias in dispersal (fig. 6; also see Weir and Schluter 2007).

Given that most of our existing insights about the macroevolutionary and biogeographic dynamics underlying the latitudinal diversity gradient come from terrestrial birds and mammals and marine mollusks (see Jablonski et al. 2006 for review), it is obviously premature to conclude that such dynamics differ in important ways between the land and the sea; the differences discussed above could simply reflect clade-specific differences. However, other independent observations also suggest that there could be interesting land-sea differences in macroevolutionary and biogeographic dynamics.

Extinctions of species in extratropical regions due to Pleistocene glacial cycles, featured so prominently in discussions of the latitudinal diversity gradient on land (e.g., Wallace 1878; Svenning 2003; Hawkins et al. 2006; Weir and Schluter 2007), may be far less important for marine taxa. While local extinctions and range expansions of marine mollusks in response to glacial-interglacial cycles are well documented (Valentine and Jablonski 1993), there is little evidence for widespread global extinctions of species during the middle or late Pleistocene (see Roy et al. 1996; Roy and Pandolfi 2005 for review). Pliocene and early Pleistocene extinctions are well documented in many marine groups, but the timing and spatial patterns of these extinctions were complex, and they involved both tropical and extratropical assemblages (see Smith and Roy 2006). This difference between marine and terrestrial groups in the timing, magnitude, and nature of putative extinctions (evidence for extinctions driven by Pleistocene glacial cycles in many terrestrial groups is indirect because of the lack of a well-preserved fossil record) could reflect the difference in the nature of the two habitats. On land, Pleistocene glaciers completely covered large areas, making them uninhabitable, and it is reasonable to assume that species that were restricted to those areas went extinct. The oceans, on the other hand, are three-dimensional, and except in some very shallow basins, the effects of Pleistocene glaciations would have been manifested largely as changes in temperature and ocean circulations rather than total habitat destruction. So it may be reasonable to postulate that, on average, marine species would have been less likely to go globally extinct as a result of the Pleistocene glaciations than terrestrial species would have. This is particularly true given the wide geographic distributions of many marine taxa and the observed correlation between bathymetric range and geographic range in marine species (Harley et al. 2003).

Both the magnitude and the pace of environmental variability also differ between land and sea. Long-term measurements have revealed that in the ocean, variance in sea surface temperature increases with the temporal scale of observation (i.e., it is red shifted), while on land, the variance stays relatively stable over time (Steele 1985; Vasseur and Yodzis 2004; Halley 2005). This implies that terrestrial organisms have to adapt to a different rhythm of environmental variation than their marine counterparts (Steele 1985; Halley 2005), which could lead to differences in population-level responses to environmental change. Similarly, long-distance larval dispersal and recruitment dynamics, so critical for marine population biology, have virtually no analogue in terrestrial animal ecology (Paine 2005). So it is not surprising that marine ecologists tend to view physical oceanographic processes as being important drivers of many ecological and biogeographic pat-

terns, from geographic distributions of species (Gaylord and Gaines 2000) to the structure and composition of communities (Gaines and Roughgarden 1985; Connolly and Roughgarden 1998). Thus, for marine organisms, traits such as larval mode that determine the ability of an organism to disperse, often passively taking advantage of oceanographic flows, play an important role in macroevolution (Jablonski 1986; Jablonski and Hunt 2006). Again, analogues of this among terrestrial animals appear to be few.

Of course, it remains an open question whether any of these differences are relevant for understanding the observed differences in macroevolutionary dynamics underlying the latitudinal diversity gradient in marine versus terrestrial clades. But the first step toward resolving the issue would be to analyze latitudinal trends in origination, extinction, and dispersal rates in marine versus terrestrial clades using the same models and similar types of data (i.e., paleontological or phylogenetic age estimates). Only such standardized comparative analyses can reveal the parameter or combination of parameters that leads to the observed differences, thereby facilitating the search for the underlying processes.

Challenges That Remain

While the models presented here highlight the role of dispersal in generating spatial gradients in diversity, estimating past trajectories and rates of dispersal for real taxa remains a major challenge. Even for clades with a good fossil record, quantifying how distributions of taxa change over time poses a difficult problem because of uneven sampling (Jablonski et al. 2006). For clades without a good fossil record, quantifying biogeographic histories of taxa generally involves reconstructing ancestral states using phylogenies (e.g., Ronquist 1997; Ree et al. 2005; Wiens et al. 2006), a potentially useful approach but one not immune to the general problems inherent in reconstructions of ancestral states (e.g., Cunningham et al. 1998). Furthermore, estimating the effects of dispersal requires comprehensive phylogenies that include taxa from multiple regions rather than region-specific phylogenies. Obviously the former presents a much larger analytical and logistical challenge, although such global phylogenies are increasingly becoming available for smaller clades (e.g., Xiang et al. 2004; Wiens et al. 2006). Similarly, estimating parameters by applying dynamic, spatial models to data on extant taxa is possible for simple models and fossil-based phylogenies that use absolute ages (Goldberg et al. 2005), but it is much harder for more detailed, parameter-rich models and molecular phylogenies.

Extinction is another critical component of many hypotheses about present-day diversity gradients (e.g., Wal-

lace 1878; Svenning 2003; Jablonski et al. 2006; Hawkins et al. 2006), and our results again underscore the importance of extinction. Yet robust estimates of extinction rates remain scarce for most groups of living organisms. Even for groups such as marine invertebrates where global extinction rates of higher taxa are well known (see Jablonski 1995, 2005), relatively few studies have quantified how regional extinction rates vary over time, especially at the species level (see Smith and Roy 2006). Obviously, hypotheses about diversity gradients cannot be properly tested without reliable estimates of how extinction rates of species and/or lineages have changed along latitude. Generating reliable estimates of past extinction rates for groups with a fossil record remains a challenge, again because of spatial biases in sampling and preservation (Jablonski et al. 2006; Valentine et al. 2006), and it is even more difficult for groups without a fossil record unless one assumes that extinction rates have been stochastically constant (Nee et al. 1994). This assumption may be violated by empirical data showing not only temporal variations in rates but also direct and indirect evidence for taxonomic and ecological selectivity (e.g., Latham and Ricklefs 1993; Todd et al. 2002; Svenning 2003; Paradis 2004; Smith and Roy 2006). Whether such variations are large enough to invalidate the assumption of stochastically constant extinction rates over long periods of time or across large regions inherent in many empirical analyses (e.g., Flessa and Jablonski 1996; Gaston and Blackburn 1996; Cardillo et al. 2005; Ricklefs 2006*b*; Weir and Schluter 2007) or in models like ours remains to be seen.

Finally, it remains an open question whether there are general rules that determine latitudinal and other diversity gradients in all taxa. Given the complex interactions among origination, extinction, and dispersal seen in the models presented here, we suspect that the relative importance of macroevolutionary versus ecological and/or biogeographic processes in generating diversity gradients is likely to be different for different clades and perhaps for terrestrial and marine organisms. However, the issue cannot even be addressed unless future studies of diversity gradients are based on consistent metrics and analytical methods. Unlike for many questions in ecology and evolution, at present there are no standard models or statistical methods that are widely used for analyses of diversity gradients (see Jablonski et al. 2006 for a review), making it impossible to compare the results of individual studies. Furthermore, some of the existing analyses of diversity gradients focus on the species level, while others emphasize clade-level dynamics (see Jablonski et al. 2006; Mittelbach et al. 2007). Given the different timescales involved, we think it is unlikely that the macroevolutionary and biogeographic dynamics are the same across different levels of the phylogenetic hierarchy. Species-level trends are more

likely to bear a signature of Plio-Pleistocene environmental changes, while the higher-taxon-level patterns have origins in deeper geological times under very different climate regimes.

Biologists and naturalists have wondered about the causes of latitudinal and other gradients in diversity for close to two centuries, but the explanations still elude us, despite increasing availability of phylogenetic and paleontological data and advances in analytical methods in recent decades. Solving the problem will require using this information and analytical methods in a consistent manner across different clades within the framework of quantitative models that include both macroevolutionary and biogeographic processes.

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