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## THE CAUSES OF SPECIES RICHNESS PATTERNS ACROSS SPACE, TIME, AND CLADES AND THE ROLE OF "ECOLOGICAL LIMITS"

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ABSTRACT

*A major goal of research in ecology and evolution is to explain why species richness varies across habitats, regions, and clades. Recent reviews have argued that species richness patterns among regions and clades may be explained by "ecological limits" on diversity over time, which are said to offer an alternative explanation to those invoking speciation and extinction (diversification) and time. Further, it has been proposed that this hypothesis is best supported by failure to find a positive relationship between time (e.g., clade age) and species richness. Here, I critically review the evidence for these claims, and propose how we might better study the ecological and evolutionary origins of species richness patterns. In fact, ecological limits can only influence species richness in clades by influencing speciation and extinction, and so this new "alternative paradigm" is simply one facet of the traditional idea that ecology influences diversification. The only direct evidence for strict ecological limits on richness (i.e., constant diversity over time) is from the fossil record, but many studies cited as supporting this pattern do not, and there is evidence for increasing richness over time. Negative evidence for a relationship between clade age and richness among extant clades is not positive evidence for constant diversity over time, and many recent analyses finding no age-diversity relationship were biased to reach this conclusion. More comprehensive analyses strongly support a positive age-richness relationship. There is abundant evidence that both time and ecological influences on diversification rates are important drivers of both large-scale and small-scale species richness patterns. The major challenge for future studies is to understand the ecological and evolutionary mechanisms underpinning the relationships between time, dispersal, diversification, and species richness patterns.*

Introduction

A MAJOR GOAL of biology is to understand the diversity of life, and how and why the number of species varies among regions, habitats, and taxonomic groups. Understanding patterns of species richness has taken on new urgency, as human activities may soon lead to the extinction of the majority of extant species (e.g., Dirzo and Raven 2003) even as the majority of extant species have seemingly yet to be described (e.g., May 1988; Wilson 1992).

Dozens of hypotheses have been proposed to explain patterns of species richness, especially variation between habitats and large-scale regions (e.g., the latitudinal diversity gradient; Willig et al. 2003; Mittelbach et al. 2007). However, ultimately, only a limited number of processes can directly change the number of species in a given group or region. In fact, there are only three (e.g., Ricklefs 1987). Species richness patterns are ultimately caused by speciation, extinction, and dispersal. Speciation creates new species and increases species richness. Extinction eliminates species (either locally or globally) and decreases species richness. Dispersal influences spatial patterns, and can add species to a given location, habitat, or region without speciation (but all species must arise through speciation ultimately). Even though various ecological, evolutionary, and biogeographic processes may influence these three processes (speciation, extinction, and dispersal), any explanation for species richness patterns must ultimately appeal to one or more of these three processes. Of course, the idea that speciation, extinction, and dispersal are the factors that directly determine species richness is hardly new, and has been present in the literature for decades (e.g., Ricklefs 1987).

Yet this idea has been abandoned in some recent literature on species richness patterns. Strangely, some of the opposition to this idea has not come from ecologists, but from evolutionary biologists (e.g., Rabosky 2009b). It has recently been suggested that "ecological limits" represent an alternative explanation to those based on the processes of speciation, extinction, and dispersal (e.g., Rabosky 2009b; see also Mittelbach et al. 2007; Ricklefs 2007; and others). Some authors have proposed that ecological limits are so pervasive that they will cause standard methods for studying the evolutionary causes of richness patterns (i.e., estimating diversification rates) to give misleading results (Rabosky 2009b). Furthermore, many papers continue to posit ecological explanations as an "alternative" to evolutionary explanations (e.g., Mittelbach et al. 2007). Finally, many ecological papers on species diversity continue to ignore evolutionary aspects of species richness patterns altogether, even though speciation is the ultimate source of species richness.

In this paper, I will argue that several important misconceptions about the causes of species richness patterns have been promulgated in the recent literature. In fact, "ecological limits" and diversification rates are not alternative paradigms. Instead, ecological limits are simply one of many potential factors that influence net diversification. I will argue that much of the evidence used to argue for ecological limits is problematic, and there is also considerable contradictory evidence. I will argue that estimates of net diversification rates can be used to help explain richness patterns, especially if a simple diagnostic test is used. I will argue that time (e.g., the time that a given clade has been present and speciating in a given region) has been inappropriately dismissed as a major cause of species richness patterns, that it has been confused with "clade age," and has mistakenly been assumed to be mutually exclusive of the effects of diversification rates. I will briefly summarize existing evidence for the major causes of species richness patterns, and how we might distinguish between them. Finally, I will outline a general approach for understanding spatial patterns of species richness that integrates ecological and evolutionary factors.

Much of my paper will address the conclusions made by Rabosky (2009b) and the evidence used to arrive at those conclusions (his being the most extensive recent paper on ecological limits). However, the present paper should be relevant to all ecologists and evolutionary biologists interested in the origins of species richness pat-

terns. I also note that despite my criticisms of Rabosky (2009b), my focus on it here illustrates its success as a thought-provoking article that has brought greater attention to an intriguing topic.

## "Ecological Limits" as an Alternative Explanation for Diversity Patterns

### a logical fallacy: ecological limits "versus" diversification rates

In a prominent paper, Rabosky (2009b) proposed that diversification rates and ecological limits are "alternative paradigms" to explaining species richness patterns. A similar hypothesis was promoted earlier by Mittelbach et al. (2007) in another prominent paper (see their Figure 1), and similar ideas have been expounded by Ricklefs (2007, 2009), Rabosky (2010), and others. Rabosky (2009b) went so far as to suggest that "ecological limits" were an alternative to speciation and extinction as an explanation for diversity patterns (e.g., he contrasts "factors that influence ecological limits relative to those that influence speciation and extinction," p. 741).

What exactly are ecological limits? Rabosky (2009b) defines ecological limits as being constraints on the number of species that can occur in a given region due to "finite resources" (p. 736), and suggests that this concept also applies to the number of species in a clade. He proposes that ecological limits are present when the number of species does not increase in a clade or region over time. However, he does not describe the specific ecological mechanisms by which ecological limits would influence species richness. This is critically important, because he does not actually describe how ecological limits could influence the species richness of a clade without influencing the rate of speciation or the rate of extinction.

In fact, for a given clade, it is simply impossible to change the number of species without changing the rates or patterns of speciation or extinction. Note that the rate of diversification is simply the rate of speciation minus extinction, or the rate of

net accumulation of species over time. Therefore, it is logically impossible for ecological limits to be an alternative to diversification rates as an explanation for diversity patterns among clades. Ecological limits can only change the species richness of clades by changing the balance of speciation and extinction over time (in other words, the net diversification rate). This is true even if these rates of speciation and extinction change dramatically over time.

In theory, ecological limits on the number of coexisting species could influence spatial species richness patterns (e.g., differences in species richness between habitats or climatic zones) by influencing dispersal, without influencing speciation or extinction (but this is not mentioned by Rabosky 2009b). This might occur by influencing dispersal, the third mechanism by which species richness changes over space. For example, along an ecological gradient, certain habitats might "fill up" with species more quickly than others, preventing species from dispersing into or persisting in those habitats. Ecological limits on local coexistence in a given habitat might, in theory, simultaneously reduce speciation, increase local extinction, and decrease dispersal (and, in some cases, failed dispersal and local extinction might be effectively indistinguishable). However, this hypothesis only pertains to spatial richness patterns, not patterns in clades, whereas clades are the major focus of Rabosky's (2009b) paper.

In summary, even if ecological limits within clades are widespread, they can only influence species numbers within a clade by influencing speciation and extinction. Therefore, ecological limits are simply another factor that potentially influences net diversification (speciation – extinction), not an alternative explanation. But are ecological limits really widespread?

### re-evaluating the paleontological evidence

The putative evidence for ecological limits on species richness bears further scrutiny. In all three of his figures, Rabosky (2009b) shows species richness as rising to a given limit within a given clade and then

remaining constant over time. In fact, the only direct evidence that could support a pattern of species richness failing to accumulate over time would have to come from the fossil record (e.g., examination of phylogenies of living taxa can only show increases in richness over time within a clade; Ricklefs 2009).

Rabosky (2009b) concludes that "the overall pattern in the fossil record is more of diversity constancy than unbounded increase (Ricklefs 2007)" (p. 737). The Ricklefs (2007) paper that is cited as evidence itself cites only three paleontological papers in support of this sweeping claim (Alroy 2000; Allen and Gillooly 2006; Jaramillo et al. 2006). In fact, all three papers are somewhat restricted in their taxonomic, geographic, and temporal scope, none focus on the species richness of a particular clade over time (e.g., mammals are a clade, but North American mammals are not), and none of these three papers explicitly shows constant species richness over time. The Alroy (2000) paper on North American Cenozoic land mammals shows increasing species richness over time (even if the increase is not exponential and unbounded), not constant richness. Allen and Gillooly (2006) focus on three groups of ocean plankton over 30 million years, and do not present analyses of species richness over time. Jaramillo et al. (2006) present data on plant species richness from 65 to 20 Million years ago (Mya) from several sites in central Colombia and western Venezuela, and show species richness increasing over time and then decreasing, in association with rising and falling temperatures (not constant richness over time). The latter two studies present evidence suggesting that changes in species richness over space (Allen and Gillooly 2006) and time (Jaramillo et al. 2006) are associated with changes in speciation rates (but recall that these studies are being used as support for the idea that speciation rates are unimportant in explaining species richness). Thus, constant diversity cannot be characterized as "the overall pattern in the fossil record" based only on these three studies cited by Ricklefs (2007).

The most extensive paleontological study cited by Rabosky (2009b) is that of Alroy et al. (2008), a massive review of data on marine animal diversity over the past ~500 million years. Based on this paper, Rabosky (2009b) concludes that "large expanses of time are characterized by no clear trend in diversity, including most of the Paleozoic and Cenozoic" (p. 737). However, there are several crucial points here. First, although not mentioned by Rabosky (2009b), diversity here actually means "number of genera," not number of species (although his title, figures, and examples all pertain only to species richness). It is not clear if or how generic diversity and species richness are related here, and the topic is simply not addressed. In fact, older studies of species richness (not generic richness) of marine invertebrates suggest instead that species richness has been increasing over the past 500 My, especially from the mid-Mesozoic to Cenozoic (e.g., Sepkoski et al. 1981; their Figures 1A, B). Second, the lack of a clear trend in diversity over this time period might be expected, given the five mass extinction events that occurred over the last ~500 My (which are known to have strongly influenced marine invertebrates; e.g., Raup and Sepkoski 1982). Third, despite some temporal fluctuations in generic diversity due to mass extinctions and other factors, generic diversity is clearly increasing over time, especially in the last 200 My (Figures 1 and 4 of Alroy et al. 2008). This trend of increasing generic diversity is most dramatic in the analysis that includes the largest number of genera (Figure 4 of Alroy et al. 2008), which suggests dramatically increasing diversity in the Cenozoic. The Cenozic is a period during which Rabosky (2009b) stated that there was no clear trend, and the trend that it does show is the opposite of that suggested by his verbal summary of the fossil record.

The strongest evidence for or against ecological limits on species richness should come from information on local species richness over time. After all, the concept of ecological limits is based on the idea of finite resources, and species cannot be reducing each others' resources if they are

not sympatric. Unfortunately, few studies seem to have addressed this topic. Knoll (1986) summarized data on 391 terrestrial vascular plant floras from 410 to 1.6 Mya, and showed that the median local species richness of terrestrial plants has increased over time in the last ~410 My (Figure 1). Bambach (1977) addressed local species richness in benthic marine invertebrate macrofossils over the Phanerozoic (Paleozoic to Cenozoic) with data from 386 communities. He showed that local richness generally increased over time in nearshore (e.g., deltas, shoreline) and open water environments (the environments containing the majority of species), especially in the Cenozoic (Figure 2). However, species richness remained similar over time in low-diversity, "stressful" environments (e.g., tidal flats, estuaries), providing a possible example of ecological limits (Figure 2). Nevertheless, the overall pattern in both plants and marine invertebrates is that local richness generally increases over time (based



Figure 1. Local Species Richness Over Time in Plants

Filled circles mean local richness across multiple sites within a given time interval, based on data from Knoll (1986). Open circles indicate estimated values for angiosperms alone (based on mean local richness of all plants and the percentage of angiosperms, Table 7.1 and Figure 7.3 of Knoll 1986). Given that species richness generally increases over time, these data do not support the idea that there are "ecological limits" on local species richness over time. The small decrease in the late Cenozoic is apparently an artifact of increased sampling of species-poor temperate communities (Knoll 1986).

on these two studies), but this is clearly an area in need of further research.

## Is There Really "No Relationship between Clade Age and Species Richness"?

Rabosky (2009b) states that the "best evidence in favour of diversity regulation" (p. 737) is the absence of a relationship between clade age and species richness. There are at least three fundamental problems with this argument.

First, negative evidence for one pattern is not positive evidence for another. The complete disconnect between the clade-level pattern and the relevant ecological and paleontological data is exemplified by angiosperms. Although angiosperm families show no relationship between clade age and clade richness (which suggests ecological limits on species richness to Rabosky 2009b), paleontological data (Knoll 1986; his Figure 7.3) show that local richness of angiosperms has increased dramatically over time through the Mesozoic and early Cenozoic (Figure 1), with no evidence of ecological limits on their local richness (the small decrease in the late Cenozoic is apparently an artifact of increased representation of species-poor temperate localities; Knoll 1986). More importantly, there is no clear theoretical prediction as to why a lack of relationship between clade ages and their species richness supports a hypothesis of ecological limits. Specifically, the absence of a positive relationship between clade age and time among clades does not show that the species richness of any given clade remained constant over time. Instead, the absence of a positive age-diversity relationship may simply indicate that different clades have increased in richness at very different rates (i.e., differences in net diversification rates among clades).

Second, Rabosky (2009b) cites only a handful of original studies that show this lack of relationship (e.g., Magallón and Sanderson 2001; Ricklefs et al. 2007; Rabosky 2009a). Most importantly, all of these studies are biased against finding a relationship between clade age and richness because they only compare clades of similar taxonomic rank, and therefore are strongly biased to-
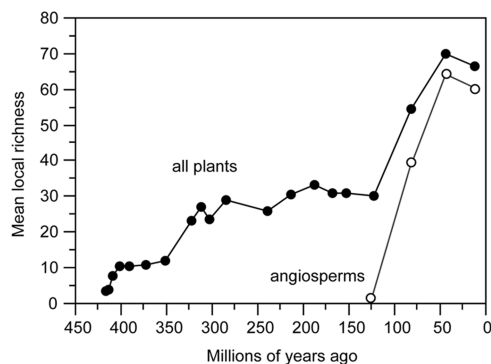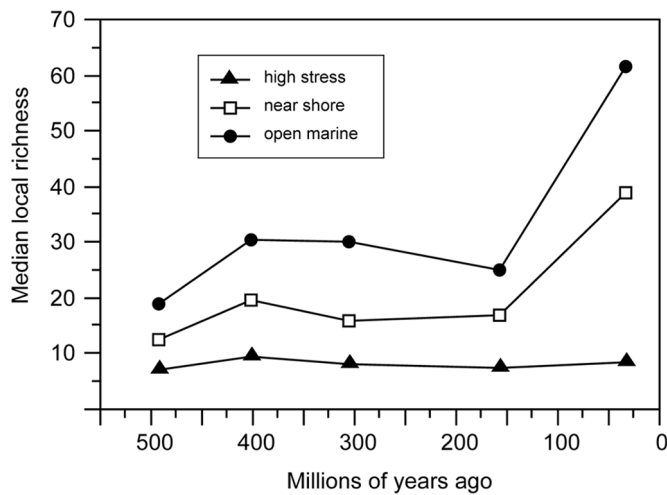
Figure 2.   Local Species Richness Over Time in Marine Invertebrates
   Each data point represents the median species richness across multiple local sites within a given time interval, based on data from Bambach (1977). Data are divided according to different habitats. Given that species richness increases over time in all but the low diversity environments (especially between the Mesozoic and Cenozoic), these data do not support the idea that there are "ecological limits" on species richness over time.

ward comparing clades of similar age. For example, in the study of 62 angiosperm families cited by Rabosky (2009b), >50% of these families are between 50 and 100 Million years old (Myo), and >85% are >40 Myo (Magallón and Sanderson 2001), hardly an unbiased sample of potential clade ages. To show that clade age is truly unimportant, an unbiased analysis should allow for comparison of (for example) non-nested orders, family, genera, and clades of species within genera, using a comprehensive (all extant species), time-calibrated phylogeny. By "non-nested" I mean, for example, that when a given genus and family are compared, the genus does not belong to that family (otherwise, the analysis could be biased in favor of a relationship between clade age and richness). It seems unlikely that such an unbiased analysis would show clade age to be unimportant.

   Third, Rabosky (2009b) does not mention in this section that the most extensive analysis (so far) of the relationship between clade age and clade richness actually showed strong support for a positive relationship across the included animal clades (McPeek and Brown 2007).

   Many of Rabosky's (2009b) conclusions about the unimportance of clade age for explaining patterns of clade richness seem to be based on his earlier analysis (Rabosky 2009a). This analysis also merits further scrutiny. Rabosky (2009a) used essentially the same data as that used by McPeek and Brown (2007), although he included plants and excluded several animal clades that were used by those authors. However, Rabosky (2009a) states that the analysis by McPeek and Brown (2007) is problematic because "there are significant age differences among the groups they considered" (p. 663). One might think that "significant age differences among the groups" would be a prerequisite for a study of the effect of clade age on richness, because if there are no significant differences, then the analysis would obviously be biased to show that clade ages are unimportant, which is just what Rabosky (2009a) shows. He then subdivides the data into smaller and smaller groups (e.g., separating insects and vertebrates, and then subdividing vertebrates), creating further biases for clades to be of similar age. These sources of bias are piled on top of the tendency to use only clades of the same rank, which are potentially biased to be of similar age (and

which may have other biases created by human ranking of clades).

Despite these potential sources of bias, Rabosky (2009a) still finds a highly significant relationship between clade age and species richness across insect orders (which goes unmentioned in his section claiming "no relationship between clade age and species richness" (p. 663); Rabosky 2009b). Although one might be tempted to dismiss this finding as "just insects," insects have long been known to contain the majority of all living described species, across all groups of living organisms (e.g., animals, plants, fungi, bacteria; Wilson 1992). Rabosky (2009b) also concludes that time is only important in "some younger clades" (p. 738), but earlier concluded that insects and vertebrates should not be included in the same analysis because "insects are much older . . . than vertebrate orders" (Rabosky 2009a:663).

In summary, previous studies show that clade age is a potentially important explanation for many species richness patterns among clades, including animals in general (McPeek and Brown 2007) and the most species-rich group of organisms (insects; Rabosky 2009a). They also show that clade age can be important in explaining the diversity of older clades as well as younger groups. However, many of these analyses of the relationship between clade age and richness have been biased by comparison of taxa of the same rank and similar age.

### diversity-dependent diversification is not evidence for "no increases in diversity over time"

As a third line of evidence supposedly supporting ecological limits on species richness over time, Rabosky (2009b) mentions paleontological studies showing faster diversification after mass extinction events (or other decreases in diversity), as well as evidence for declining rates of lineage accumulation within clades of living taxa over time (e.g., Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008). However, showing increases and decreases in diversification rates at different points in time is not evidence that species richness cannot con-

tinue to accumulate in these clades over time. In other words, these studies show evidence for speedups and slowdowns, but Rabosky's (2009b) figures and speculations about ecological limits are all based on the assumption of a complete stop in the accumulation of species richness over time. Therefore, these studies are not direct evidence for ecological limits on species richness over time.

### Ecological Evidence Against Ecological Limits

Rabosky (2009b) does not describe how "ecological limits" would actually work in terms of ecological and evolutionary processes. Nevertheless, a fundamental assumption of the hypothesis of ecological limits is that finite resources are somehow preventing the accumulation of species over time. If this is true, the arena in which ecological limits should play out is at the local scale (i.e., species occurring in different regions presumably are not reducing each others' resources). However, ecological studies of extant taxa do not necessarily support the idea that local diversity is limited over time by finite resources.

If local richness was limited, local richness within a clade might be expected to converge across sites in different regions, regardless of the size of the regional pool. However, there is a rich literature in ecology showing that local richness tends to be correlated with the size of the regional species pool, and that "saturation" of local communities with species is not the common pattern (e.g., Ricklefs 1987; Caley and Schluter 1997; Hillebrand and Blenckner 2002; Karlson et al. 2004; Shurin and Srivastava 2005; Freestone and Harrison 2006; Cornell et al. 2008; recent review in Harrison and Cornell 2008). Many of these studies involve local sites in different regions with similar environments (e.g., Cornell et al. 2008), suggesting that the differences in local richness do not simply reflect the impact of local environmental conditions. Although the interplay between local richness, regional richness, and clade diversification is complex and underexplored (see Harrison and Cornell 2008), this literature

suggests that local communities are not generally saturated with species due to finite resources, and it should not be ignored.

Furthermore, phylogenetic studies in turtles and bats (e.g., Stephens and Wiens 2003; Stevens 2006) suggest that local diversity is correlated with the amount of time that the group has been present in the region in which the local site is imbedded. In other words, these studies suggest that local communities do not "fill up" with species over time. In bats, one could argue that local richness might be higher because tropical conditions permit more species to coexist than in the temperate zone (rather than because temperate regions have been colonized more recently). However, in emydid turtles, local diversity is higher in their ancestral temperate zone than in the recently colonized tropics, even though ecological studies suggest that emydids thrive in tropical climates (Stephens and Wiens 2003).

Studies of invasive species also offer (indirect) evidence against the idea that regions and communities have generally reached ecological limits on the number of species they can support. For example, invasive plant species on islands generally increase plant richness (Sax and Gaines 2008). In fact, exotic species typically double overall plant richness on the islands where they occur (Sax and Gaines 2008).

If the mechanism underlying ecological limits involves competing species that set each others' range limits (e.g., given that clades with larger geographic ranges may have higher species richness; Rabosky 2009a), then one might attempt to argue that local-scale richness was irrelevant. But this mechanism presumably still requires that local communities be saturated and unable to support additional species. Otherwise, there is no reason why one species could not enter the range of a potential competitor.

## Should We Expect Ecological Limits on Diversity?

Rabosky (2009b) argues that limiting ecological resources will lead to no net increase in species richness over time within clades and regions. However, there are several reasons why limiting ecological resources might not actually prevent the number of species from continuing to accumulate over time.

First, species can potentially evolve to utilize different ecological resources to reduce ecological overlap between species. This is a fundamental concept of the ecological theory of adaptive radiation (Schluter 2000). Although there may be constraints on the extent to which a given clade can evolve new ecological roles over time, whether such constraints ever lead to ecological limits on species richness over time remains unclear. In fact, some ecologists have argued that "there are no grounds for the belief that species interactions set an absolute upper limit to diversity at any scale" (Loreau 2000:73).

Second, even if species are somehow limited in their ecological divergence from each other, it is not so clear that ecologically similar species cannot occur together. In fact, recent theory suggests that ecological similarity between species may actually enhance their ability to occur in sympatry (review in Mayfield and Levine 2010). For example, species with similar ecological traits may tend to have similar competitive abilities, making it more difficult for one species to eliminate another, and facilitating their occurrence in sympatry over very long time scales (e.g., Scheffer and van Nes 2006). In fact, recent studies have shown that closely related, sympatric clades can undergo parallel patterns of phenotypic diversification, leading to local communities in which species from different clades are actually more similar to each other than expected by chance (e.g., Kozak et al. 2009), the opposite of the pattern expected if there are ecological limits on the co-occurrence of similar species.

Third, research on speciation modes suggests that new species are typically generated in allopatry (e.g., Barraclough and Vogler 2000; Coyne and Orr 2004; Phillimore et al. 2008; Hua and Wiens 2010). Thus, newly formed species should generally have no ecological impact on each other at all, and so (at least in some cases)

the number of co-occurring species and limiting ecological resources may actually be irrelevant to the accumulation of new species in the clade or region.

Clearly, theoretical studies are needed to explicitly assess whether ecological limits on species richness over tens of millions of years are a realistic expectation (and under what conditions). The study by McPeek (2008) is an important step in this direction, although it does not directly address species richness over time and makes some important assumptions (e.g., no allopatry, such that all ecologically similar species potentially interact). In summary, at present, there seems to be little theoretical or empirical basis for assuming that strict ecological limits on species richness over time are generally widespread.

## Estimating Diversification Rates to Study Diversity Patterns

Given the dependence of species richness on speciation and extinction, many studies that have addressed the evolutionary origins of species richness patterns have considered the diversification rate of clades. The diversification rate of a clade is often estimated as the log of the number of species in the clade divided by the age of the clade, with some variations (e.g., Magallón and Sanderson 2001) designed to better account for the possible effects of extinction (review in Ricklefs 2007). For example, several studies have examined whether clades occurring in the tropics tend to have higher diversification rates than temperate clades (e.g., Cardillo et al. 2005; Ricklefs 2006; Wiens et al. 2006, 2009; Wiens 2007; Jansson and Davies 2008; Svenning et al. 2008). The underlying idea is that factors that promote speciation and/or extinction in certain environments will cause clades that occur in those environments to generally have higher net diversification rates. Note that here I use "diversification rates" to mean "net diversification rates" (focusing on the number of species that have accumulated from the origin of the clade to the present day, and not the estimated rate at some particular point in the past).

One of the conclusions that Rabosky (2009b) "demonstrates" from his speculations about ecological limits is that it may be inappropriate to estimate diversification rates and use these estimates to study diversity patterns. He argues that if clades reach their "ecological limits" and stop accumulating species over time (if this is possible), then it is misleading to compare diversification rates between groups, despite the many studies that have done so (including a study coauthored by Rabosky, published in the same month; Alfaro et al. 2009). In fact, these conclusions are somewhat problematic.

For example, Rabosky (2009b) argues that if one clade has higher ecological limits (carrying capacity) than another, it will have more species and therefore a higher estimated diversification rate (his Figures 2a, b). He considers this to be misleading, but the fact that ecological conditions permit one clade to have a greater net accumulation of species over time is exactly the sort of pattern that such analyses are designed to reveal (e.g., ecological conditions in the tropics lead to higher diversification rates in tropical clades). Similarly, Rabosky (2009b) argues that estimates of diversification rates will be misleading if two groups have the same maximum number of species, but one is younger than another. But the fact that the younger clade reached this maximum more quickly is also what the estimate of diversification rates will and should reveal.

Estimates of diversification rate are typically used as estimates of the net diversification in a clade over time, which are then used to compare among clades. It is clear that species do not necessarily accumulate at a constant rate over time within a clade, as speciation and especially extinction may be infrequent, episodic, and stochastic. The fact that different environments may allow different numbers of species to accumulate and persist over time is precisely what these analyses are designed to reveal (e.g., a relationship between latitude and diversification rate; Cardillo et al. 2005; Ricklefs 2006; Wiens 2007; Jansson and Davies 2008; Svenning et al. 2008). Further, the observation that a single estimated diversification rate across multiple clades fits

a set of observed data poorly (e.g., Rabosky 2010) is not evidence that estimated diversification rates are generally useless or that ecological limits are present. Instead, it merely suggests that separate diversification rates should be estimated for each clade (as is typically done).

Rabosky (2009b) suggests that lack of a positive relationship between clade age and species richness invalidates attempts to use diversification rates to understand richness patterns (even though variation in diversification rates among clades seems the most likely cause for this relationship being absent). But perhaps the more important question is whether there is a relationship between diversification rates of clades and their species richness. If there is such a relationship, then variation in diversification rates are presumably relevant for explaining species richness patterns among clades, regardless of any relationship between the ages of clades and their diversification rates. This suggests a simple diagnostic test for analyses using diversification rates: if diversification rates of clades are positively correlated with the richness of those clades, then diversification rates may help explain those patterns. Alternately, diversification rates and species richness of clades may be uncorrelated or negatively correlated (e.g., if most clades with high diversification rates are young and have low richness, conditions usefully highlighted by Rabosky 2009b). This simple test should allow detection of cases in which net diversification rates do not generally reflect the underlying causes of diversity patterns.

Similarly, if diversification rates explain diversity along some environmental gradient (e.g., latitude), then high diversification rates should be correlated with that environmental variable. The many studies that have found evidence of higher diversification rates in tropical clades in groups with higher tropical diversity (e.g., birds, amphibians, palms; Ricklefs 2006; Wiens 2007; Svennig et al. 2008) would seem to be strong evidence against the idea that diversification rates are generally "misleading" about species richness patterns. Presumably, these statistically significant correlations between diversification rates and envi-

ronmental variables did not simply come about by chance.

The fact that in some groups variation in diversification rates is not aligned with patterns of species richness (e.g., Wiens et al. 2006, 2009) does not necessarily mean that these estimated diversification rates are generally "meaningless." It may simply mean that variation in diversification rates is not supported as an explanation for the diversity pattern in question, and that these patterns are therefore more likely to be explained by some other factor instead. For example, in some groups in which latitudinal position and diversification rates of clades are uncorrelated, there is strong support for the hypothesis that high tropical richness is instead related to greater time spent in tropical regions (e.g., Wiens et al. 2006, 2009).

My point in this paper is not that current methods for estimating diversification rates are perfect, or that they are always perfectly applied in the studies that use them. Instead, I argue from first principles that variation in richness among clades must be explained by time and/or variation in the balance of speciation and extinction over time (net diversification). The idea of ecological limits on richness within a clade is not an alternative explanation, but is simply another potential factor that influences the net diversification rate of the clade. Improvements in understanding the evolutionary causes of species richness patterns will come from improving our estimation of rates and patterns of diversification (and their correlates), and not from abandoning the principle that the balance of speciation and extinction over time determines the species richness of clades. Variation in diversification rates within clades over time is simply one of many nontrivial issues to be dealt with in analyses of diversification. This issue might be dealt with in a variety of ways, including subdividing clades (or abandoning higher clades altogether and using the species-level phylogeny) or estimating rates at different slices in time from a time-calibrated phylogeny. New methods may well be needed. But the simple idea that ecology limits the richness of some clades

over time does not necessarily require a correction at all, as this is the type of pattern that an analysis of ecological factors and estimated net diversification rates is designed to reveal.

## Nonsense and Rabbits

Rabosky (2009b) proposes no specific ecological mechanism for how ecological limits would constrain species richness over time. What he does present is an analogy based on rabbits on an island, which reach a carrying capacity of 1,000 individuals. Rabosky (2009b) argues that species in a clade are like individuals of rabbits on an island, and so estimating a rate of diversification is "nonsense" because it will only depend on how old the clade is. However, this analogy has some potential weaknesses.

Let us assume first that this is a perfect analogy for the diversification of a clade. The problem is that it is a problematic analogy for a study of diversification rates and species richness patterns. Few studies, if any, are designed to estimate the diversification rate of a single clade in a single place. In fact, estimates of diversification rates are primarily interesting in a comparative sense. Do some clades have unusually high diversification rates? And if so, why? Do clades in some regions or habitats have higher diversification rates? So, to make the rabbit analogy relevant, what we would presumably do is compare the number of rabbits on different islands, which might differ in ecological characteristics that influence their carrying capacities and population sizes (e.g., area, habitat heterogeneity), and how quickly they reached those carrying capacities (e.g., have rabbits been on the island for days or decades?). So a relevant analogy would involve comparing the number of individuals on different islands relative to how long rabbits have been present on each island, and testing whether the relationship between these variables is related to the ecological characteristics of islands (i.e., analogous to testing how diversification rates are related to ecological variables).

The next question is: do rabbits on an island offer a good analogy for the diversification of a single clade? The answer is clearly "no." Perhaps the most problematic aspect of this analogy is that it implicitly assumes 1,000 ecologically equivalent species living in sympatry. But what the study of adaptive radiation shows is that clades often diversify as they evolve new ecological traits to avoid competing which each other, and thus invade new niches and adaptive zones (e.g., Schluter 2000). Given enough time to generate 1,000 species, it is unclear why rabbits on an island would not diversify ecologically (e.g., to produce carnivorous, volant, and aquatic bunny ecotypes). Following Rabosky's (2009b) argument backwards in time, the entire diversity of life should consist of a fixed, standing number of one-celled species that have remained ecologically identical for the past 3.5 billion years. Instead, the diversity of life has increased over time because organisms have been evolving new ways to exploit the environment and each other.

Proponents of ecological limits may protest that they meant all along that species richness could increase after environmental perturbations, extinction of competitors, invasion of new regions or habitats, or evolution of traits allowing use of new resource-related niches. But it is unclear when, if ever, all of these processes will be absent during the history of a clade (which raises the question of whether it is realistic to expect constant diversity in a clade over time in the first place).

## Alternatives to Diversification Rates?

Based on his critique of estimated diversification rates, Rabosky (2009b) proposes a "new" measure for use in cases in which clade age and species richness are uncorrelated. This is called omega, but in the end is simply log-transformed species richness (and in fact, dividing log-transformed species richness by clade age to estimate diversification rates ostensibly corrects for the effect of clade age on richness when comparing richness of clades of different ages). This measure of observed species richness seems to predict observed species richness well (Rabosky 2010), at least using data from ants (Pie and Tschá 2009). But,

in the end, patterns of clade richness must instead be understood by revealing the ecological, biogeographic, and evolutionary correlates of richness and diversification and understanding how variation in rates and patterns of speciation and extinction drive those patterns (see below).

## TIME AS AN EXPLANATION FOR DIVERSITY PATTERNS

All other things being equal, species richness within a clade should increase over time, as speciation adds new species to the group (e.g., McPeek and Brown 2007). This same principle might also apply to different geographic regions, latitudinal zones, and different habitats within a region, where locations that have been occupied by a group for a longer period may tend to accumulate more species, simply due to greater time for speciation to occur (the "time-for-speciation effect"; review in Stephens and Wiens 2003). Of course, all things are not always equal, and various other factors may explain species richness patterns instead, particularly variation in diversification rates over space, time, and among clades (i.e., due to conditions influencing speciation and/or extinction). The importance of time has only rarely been tested, but has been supported for many types of species richness patterns, from the global to the local scale (see below). Yet, the idea that time is a major driver of richness patterns has been largely dismissed in some recent reviews (e.g., Mittelbach et al. 2007; Rabosky 2009a,b). I will argue here that this dismissal is premature and not supported by the available evidence. Before I do, it is important to clear up a fundamental misconception.

## CLADE AGE VERSUS THE TIME-FOR-SPECIATION EFFECT

Rabosky's (2009b) paper contains an important misconception about how time and geographic patterns of species richness are related. He implicitly equates "clade age" with the time-for-speciation effect, but they are not the same thing, and confounding them may have serious con-

sequences. He suggests that the importance of time for species richness patterns should be assessed by examining the relationship between the ages of clades of similar rank (clade age) and their species richness, and possibly considering the latitudinal position of these clades (p. 740). But the timing of biogeographic dispersal to different regions may have nothing to do with named clades and their ages. Instead, the relevance of the time-for-speciation effect to spatial richness patterns must be assessed by estimating how long the group in question has been present in each relevant region or habitat (e.g., using biogeographic or habitat reconstruction on a time-calibrated phylogeny; Wiens et al. 2006, 2007, 2009; Smith et al. 2007; Kozak and Wiens 2010a). For example, within two of the most species-rich families of frogs (Hylidae, Ranidae), most higher taxa (e.g., subfamilies, tribes) are predominately tropical, and the invasions of temperate regions seem to have occurred much more recently within these higher clades, for example, among genera (e.g., Wiens et al. 2006, 2009). The recent timing of these temperate invasions seems to explain low temperate richness in these groups, and conversely, greater time-for-speciation in the tropics explains high tropical richness. But these patterns would be largely invisible to the clade-age approach using higher taxa, biasing the approach against supporting the time-for-speciation effect. In fact, major biogeographic shifts need not correspond to named clades at all (e.g., within the treefrog genus *Hyla*, there has been dispersal into North America, Europe, Middle America, and two invasions of Asia; Smith et al. 2005). As one example (Figure 3), taking the ranid data from Wiens et al. (2009), there is no significant relationship between clade ages and species richness (based on the age and diversity of the 13 subfamilies), but there is a strong time-for-speciation effect (based on the timing of biogeographic colonization of each major region). In summary, by focusing only on the age and richness of named higher taxa, Rabosky (2009b) confounds clade ages and the time-for-speciation effect, and the clade-age approach may be biased
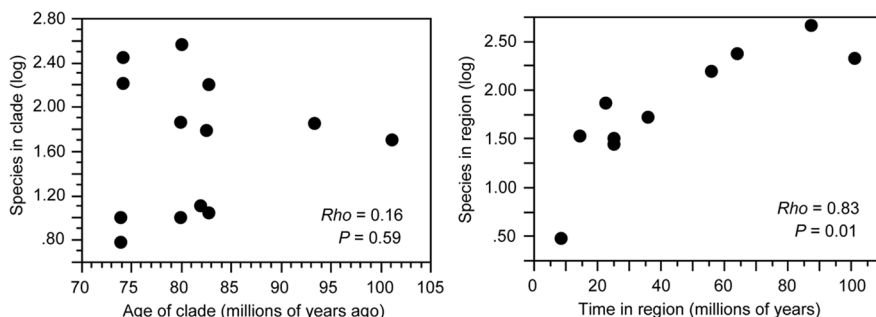
FIGURE 3.  SPECIES RICHNESS, CLADE AGE, AND THE TIME-FOR-SPECIATION EFFECT IN RANID FROGS
    Some authors have advocated using the relationship between the ages of higher taxa and their species richness to determine whether time is important in determining large-scale regional species richness patterns (e.g., Rabosky 2009b). However, these results show that in ranid frogs, there is no significant relationship between ages of higher taxa (subfamilies) and their species richness, but there is a significant relationship between the inferred first timing of colonization of each region by ranids and ranid species richness in that region (time-for-speciation effect). Thus, merely examining the relationship between clade ages and richness may conceal the importance of time for explaining spatial species richness patterns. Data on species richness, clade ages, and the timing of colonization of each region are from Wiens et al. (2009). Analyses are based on Spearmann's rank correlation, with species richness log10-transformed, and using stem-group ages of clades, all following Rabosky (2009a).

against showing the importance of time in explaining species richness patterns.

### SPATIAL PATTERNS OF SPECIES RICHNESS

There is evidence accumulating that the time-for-speciation effect may be important for explaining many spatial diversity patterns. For example, there is now evidence that the time-for-speciation effect may help explain high tropical species richness in New World treefrogs (Hylidae; Wiens et al. 2006), Old World frogs (Ranidae; Wiens et al. 2009), and New World bats (Stevens 2006). Conversely, it may explain high temperate richness and low tropical richness in emydid turtles (Stephens and Wiens 2003) and in some treefrogs (Smith et al. 2005) and snakes (Pyron and Burbrink 2009). The time-for-speciation effect also seems to explain high regional species richness at intermediate elevations (i.e., the widespread mid-elevation diversity hump) in clades of Middle American treefrogs (Smith et al. 2007) and salamanders (Wiens et al. 2007), Asian fish (Li et al. 2009), and North American salamanders (Kozak and Wiens 2010a). In almost all of these studies, it was found that variation in diversification rates along these same ecological gradients did not explain these patterns (two exceptions were Stevens (2006) who did not test for this, and Smith et al. (2007) who also found some support for diversification rates influencing richness patterns). Thus, in most of these studies, the time-for-speciation effect was supported and variation in diversification rates was not. Other studies have found evidence for the importance of the time-for-speciation effect along other ecological axes, such as predation regimes in larval damselflies (e.g., Brown et al. 2000) and climatic gradients in birds (e.g., Rangel et al. 2007), using somewhat different approaches.

In their review of the causes of the latitudinal diversity gradient, Mittelbach et al. (2007) generally dismissed the time-for-speciation effect. They described studies that found some support for it (e.g., Wiens et al. 2006), but nevertheless concluded that "[a]ll of this suggests that while tropical habitats have indeed existed longer than temperate ones, the longer duration by itself does not explain the latitudinal diversity gradient" (p. 319). Similarly, in the abstract of this paper, they mention that studies support the importance of diversification rates, but

none that support the importance of time. Furthermore, diversification rates and the time-for-speciation effect need not be mutually exclusive (e.g., Jablonski et al. 2006 (for genera); Smith et al. 2007), and the challenge is then to determine quantitatively which is more important in explaining richness patterns. Yet, most of the studies that they cited as supporting the importance of diversification rates in explaining the latitudinal diversity gradient (e.g., Ricklefs 2006) did not test for a geographic time-for-speciation effect at all. Thus, Mittelbach et al. (2007) seemingly concluded that hypothesis "a" (diversification rates) was more important than "b" (time), based largely on studies that tested for "a" but did not address "b," and dismissed studies that tested for both and supported "b" and not "a" (e.g., Wiens et al. 2006).

Rabosky (2009b) downplayed time as well, but acknowledged that time might be important in "some younger clades . . . (Wiens et al. 2006, 2009)" (p. 738). However, these "younger" clades cited are actually ~65 Myo (Hylidae; Wiens et al. 2006) and ~100 Myo (Ranidae; Wiens et al. 2009).

Time Versus Diversification Rates

In this paper, I have reviewed many studies showing that both time and diversification rates are important explanations for species richness patterns. Although Rabosky (2009b) implies that neither is important, an explanation based on "ecological limits" is indistinguishable from the traditional idea that ecology influences diversification rates. Given that both time and diversification rates are relevant, an obvious question to ask is: which is generally more important in explaining species richness patterns?

Of course, the answer depends on the particular richness pattern and the particular group. Nevertheless, two of the largest geographic patterns in species richness may be explained more by diversification rates than by time. On the other hand, many smaller-scale patterns may be explained more by time than by variation in diversification rates.

Perhaps the best-known gradient in spe-

cies richness is between tropical and temperate regions. Mittelbach et al. (2007) contrasted hypotheses based on higher diversification rates in tropical clades with those based on "time and area," with area referring to the greater area of tropical regions in the recent geological past (~30-40 Mya) and earlier. As described above, Mittelbach et al. (2007) favor those based on diversification rates over those based on time and area. However, hypotheses based on "diversification rate" and "area" are not entirely distinct. If we consider why larger areas have more species at the global scale, then the answer must be: because clades living in larger areas will have higher diversification rates, either because larger areas promote speciation and/or help reduce extinction (e.g., Fine and Ree 2006). Thus, "greater area in the past" is one of many potential causes of higher diversification in the tropics, not an alternative explanation. Furthermore, hypotheses based on time suggest that there are more species in the tropics because more clades originated there, but even proponents of time acknowledge that there must be an explanation for why more clades originated in the tropics in the first place (e.g., Wiens and Donoghue 2004). Thus, even hypotheses based on time may have to appeal to diversification rates eventually. Of course, there are many other potential explanations for why diversification rates are higher in the tropics (review in Mittelbach et al. 2007), and hypotheses based on larger area can potentially be rejected based on various lines of evidence (e.g., if diversification rates are generally higher in tropical clades, and if these clades are typically younger than ~30–40 Myo, such that they originated after tropical regions shrunk in area). Overall, given that hypotheses based on time and area are also related to net diversification rates, it seems likely that this rate variation may ultimately drive the latitudinal diversity gradient (as concluded by Mittelbach et al. 2007), and the future challenge may be to distinguish among the many possible explanations for latitudinal variation in net diversification rates.

Apart from the latitudinal gradient, one of the most dramatic gradients in species

richness across the biosphere is between marine and terrestrial environments. This gradient may also be explained by differences in net diversification rates. Marine environments cover a much greater area of the Earth's surface ($\sim$70%) than terrestrial environments, but harbor only a fraction of estimated global species richness (5-15%; for recent review see Vermeij and Grosberg 2010). Yet, phylogenetic and paleontological evidence suggest that animals (the most species-rich groups of organisms) are ancestrally marine: the basal clades of animals (i.e., those closest to the root of the tree) are primarily marine (i.e., Porifera, Cnidaria, Ctenophora, Placozoa; Halanych 2004) strongly suggesting that this is the ancestral environment, and marine animal fossils predate terrestrial fossils by more than 150 million years ($\sim$575 versus 414 Mya; e.g., Jeram et al. 1990; Narbonne 2005). Land plants were also apparently derived from aquatic (freshwater) ancestors (e.g., Waters 2003; Lewis and McCourt 2004). Given that terrestrial environments are seemingly not ancestral for animals or plants, the time-for-speciation effect cannot explain higher terrestrial diversity, and it must be explained by higher diversification rates in terrestrial clades instead. Much of this higher terrestrial diversity may have been driven by Cretaceous and Tertiary diversification of angiosperms and insects (review in Vermeij and Grosberg 2010). However, these hypotheses have yet to be tested with an explicit analysis.

On the other end of the spectrum, many smaller-scale patterns may be explained by time rather than variation in diversification rates (as implied by Rabosky 2009b). For example, many smaller-scale patterns of species richness may result from species filtering into local communities from a regional species pool across an environmental gradient. Even if the size of the regional species pool in different environments is influenced by variation in net diversification rates, variation in richness may still be explained by ecological constraints on dispersal and limited time for speciation to homogenize species richness across environments. In support of this, there does seem to be evidence for time-for-speciation effects on different habitats within regions,

including different elevations (e.g., Wiens et al. 2007; Li et al. 2009; Kozak and Wiens 2010a) and predation regimes (Brown et al. 2000). Thus, even though diversification rates may be more important in explaining some of the largest-scale patterns, time may still be critically important in explaining any given pattern in any given group. Of course, these generalizations must be rigorously tested, and the limits of when each factor will be more important remains to be seen. In fact, there is also evidence that time can be important at large spatial and temporal scales (e.g., Wiens et al. 2006, 2009) and that diversification rates can vary across habitats within a region (e.g., Smith et al. 2007).

## Ecology and Evolution of Species Richness Patterns

The preceding sections have contained very little discussion of ecology. In fact, much of the recent literature on species richness patterns is not very integrative. For example, Rabosky (2009b) proposes that the hypothesis of ecological limits is supported if there is no relationship between clade age and species richness of clades (p. 740), but without incorporation of any ecological data whatsoever. Conversely, many ecological studies of richness patterns fail to consider the evolutionary origins of species and species richness.

Species richness patterns are created by the interplay of ecological and evolutionary processes. For example, patterns of species richness along an environmental gradient must be determined by rates and patterns of speciation, extinction, and dispersal (e.g., Ricklefs 1987). But presumably ecological factors associated with this environmental gradient must influence these rates and patterns of speciation, extinction, and dispersal. Otherwise, the species richness patterns should not be concordant with the environmental gradient.

A critical point is that showing that species richness correlates with ecological variables does not mean that evolutionary factors are not involved. Even if there is a perfect relationship between ecological variables and richness, this climate-diversity relationship must still be ex-
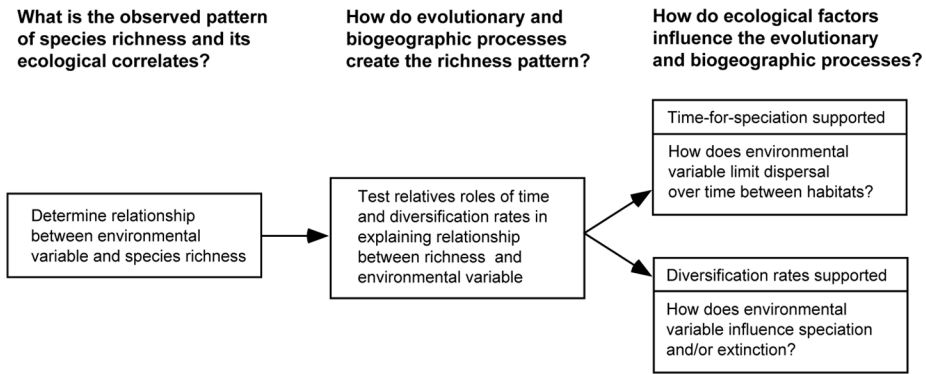
Figure 4.  A General Framework for Understanding Spatial Patterns in Species Richness
   Note that speciation, extinction, and dispersal are considered "evolutionary and biogeographic processes" for the purposes of this figure, but they can (and should) be considered ecological processes as well.

plained by the influence of the ecological variable on speciation, extinction, and/or dispersal (e.g., Wiens and Donoghue 2004).

Here I present a general framework for understanding spatial species richness patterns by integrating both ecological and evolutionary perspectives (Figure 4). To begin, we assume that species richness for a given group (clade) of organisms varies strongly along an environmental gradient (e.g., climate, latitude, elevation, predation, disturbance). The first question to address is: is the higher species richness at one end of the gradient caused by (a) greater time-for-speciation in those environments and/or (b) faster net rates of diversification in those environments (either due to increased speciation, reduced extinction, or both)?

A relationship between time and richness can be tested by obtaining a time-calibrated phylogeny for the clade and data on the distribution of each species in the clade along the gradient. It is then possible to reconstruct approximately how long the group has been present at different parts of the gradient, by mapping the distribution of the environmental variable on the phylogeny. The time-for-speciation hypothesis predicts a strong correlation between the approximate amount of time that the group has been present in each major segment of the gradient (e.g., dividing the gradient into bins of equal size)

and the number of species in each major segment of the environmental gradient (typically after log transforming the number of species).

Of course, there are many potential sources of error in an analysis of this type, but it should generally be possible to test the robustness of the results to each one. For example, there are many sources of error in reconstructing the ages of clades (but a range of ages of can be used to address the sensitivity of the results), there are many ways to characterize the distribution of each species along an environmental gradient (e.g., mean, minimum, and maximum, but the robustness of the results can be tested), and there are many potential issues in reconstructing ancestral trait values (but a variety of increasingly sophisticated models for these reconstruction methods can now be used). Further, reconstruction methods may be biased to reconstruct as ancestral the environment that is most common among species (but robustness to this source of bias can be tested using simulations; Kozak and Wiens 2010a) and effects of the environment on diversification may influence reconstruction of that variable (but methods exist to test for these effects; i.e., BiSSE, Maddison et al. 2007).

A relationship between the environmental variable and diversification rates can be tested in two general ways. First, if all or

most of the relevant species are included in a time-calibrated phylogeny, the relationship between the environmental variables and diversification rate can be tested directly using various methods, including new methods that can incorporate continuous variables (e.g., Freckleton et al. 2008; FitzJohn 2010).

Second, if only some species are included in the phylogeny, but the species richness of subclades within the group are known (e.g., if a genus is known to have 10 species but only three are included in the tree), it is possible to estimate the diversification rate for these subclades, given their estimated ages and known diversities (e.g., taking the log of the number of species divided by the age, and variations on this theme; Magallón and Sanderson 2001; Ricklefs 2007). Then, the values for the subclade for the environmental variable can be summarized (e.g., a mean of species means, a midpoint of the range of species values, or other approaches). Finally, the relationship between diversification rates and environmental variables can be tested, for example, using phylogenetic generalized least squares (e.g., Martins and Hansen 1997) to account for the phylogenetic relatedness and statistical nonindependence of subclades. If there is a significant relationship, it is important to confirm that the variation in net diversification rates is actually concordant with the richness patterns, and that diversification rates are significantly correlated with the species richness of subclades (see above).

The analyses described above should address whether the richness patterns along the environmental gradient are determined by time or variation in diversification rates. However, it is possible that both will show significant effects. Disentangling the relative contribution of each of these two factors when both seem to contribute to a gradient may not be trivial and remains an important area for future research. Yet, so far, most studies that have tested for both have found strong support for one and not the other (e.g., time and not diversification rates; Wiens et al. 2006, 2007, 2009; Kozak

and Wiens 2010a; versus both in Smith et al. 2007).

Further, these analyses are really only the beginning, and serve to set the stage for more detailed ecological analyses (Figure 4). For example, if the time-for-speciation effect primarily explains diversity along the environmental gradient, one obvious question is: what prevents dispersal from simply homogenizing diversity along the gradient? One general explanation is niche conservatism, such that species will tend to remain in their ancestral environment over time as the clade diversifies (review in Wiens et al. 2010). This hypothesis can be tested in various ways (e.g., testing which variable(s) set species range limits, and testing for an evolutionary pattern of conservatism for this variable on the tree using phylogenetic model-comparisons, as in Wiens et al. 2006; Kozak and Wiens 2010a). However, even if niche conservatism is supported, the question remains as to what population-level processes underlie niche conservatism in a particular case (e.g., competition, lack of genetic variation for traits allowing a niche shift, stabilizing selection, homogenizing gene flow; review in Wiens et al. 2010). It is also important to know why the clade arose at one end of the environmental gradient and not the other. Answering this latter question may lead to deeper phylogenetic levels than the initial clade, and possibly back to the relationship between the environmental variable and diversification rates.

Similarly, if a relationship between the environmental variable and net diversification rates is supported, this is also merely the beginning for future ecological and evolutionary research. When a relationship between diversification rates and an environmental variable is found, one of the first questions to address is: does the variable enhance speciation, reduce extinction, or both? Accurately parsing out the contributions of differences in speciation and extinction rates to differences in diversification rates from phylogenetic information is notoriously difficult (e.g., Ricklefs 2007), but simulation-based tests of new methods suggest that it may not be impossible (e.g., FitzJohn et al. 2009).

Another question to address is: how exactly might the environmental variable influence diversification rates? For example, several studies have shown that latitude is correlated with diversification rates in some groups (e.g., Cardillo et al. 2005; Ricklefs 2006; Weir and Schluter 2007; Wiens 2007; Jansson and Davies 2008; Svenning et al. 2008). But latitude itself almost certainly does not directly influence diversification, and instead, some environmental factor(s) that varies with latitude does. In fact, few of the studies that have shown that diversification rate varies with latitude have addressed what it is about lower latitudes that drive higher diversification rates.

As one example, in plethodontid salamanders, studies have shown that diversification rates are generally higher in the tropics (Wiens 2007; Adams et al. 2009). Other studies have shown that these tropical clades with high diversification rates have higher rates of climatic-niche evolution (Kozak and Wiens 2010b). Analyses also show that there is greater divergence in climatic distributions between tropical sister species relative to temperate pairs (Kozak and Wiens 2007), suggesting that these climatic differences may drive tropical speciation. The greater divergence in climatic distributions between tropical sister species seems to be associated with more limited temperature seasonality (Kozak and Wiens 2007), such that species at different elevations in the tropics experience more distinct climatic regimes than those in the temperate zone (consistently low temperatures at high elevations and high temperatures at low elevations in the tropics versus high and low temperatures at different parts of the year at all elevations in the temperate zone; e.g., Janzen 1967). Thus, the manner in which latitude, climate, and diversification interact is somewhat counterintuitive, and is not related to a specific set of tropical environmental conditions.

## Future Research

Future research on species richness patterns might usefully incorporate the three-step program described above (Figure 4). The first step is to determine the ecological correlates of species richness patterns for a given group of organisms at the scale of interest (e.g., global, regional, local, different habitats, or microhabitats). For example, is species richness (at a given scale) in Australian turtles associated with climatic variables? The second step is to use phylogenetic approaches to determine whether the richness pattern is associated with higher diversification rates or with the time-for-speciation effect, or both, as described above. The third step is to understand how the original ecological variable influences either time (e.g., by limiting dispersal between habitats or regions) or diversification rates (e.g., by promoting speciation and/or buffering against extinction). A critical point here is that the study of patterns of species richness begins and ends with analyses emphasizing ecology. But the middle step, incorporating the phylogeny, is essential to relate the species richness patterns to the processes that change species numbers (speciation, extinction, and dispersal) and inform the basic questions in the final phase of research. Of course, the general framework described here is just one of many possible approaches to studying species richness patterns that integrates both evolutionary and ecological factors.

## Conclusions

A central goal of biology is to understand the causes of differences in species richness between clades, regions, and habitat types. Species richness is directly influenced by speciation, extinction, and dispersal. Yet, it has recently been proposed that "ecological limits" on diversity offer an alternate explanation to those based on speciation and extinction, that the presence of ecological limits invalidate attempts to use estimates of diversification rates to understand diversity patterns, and that the time available for speciation (within a clade or region) is of minor importance in explaining diversity patterns. I argue that ecological limits can only change species richness in a clade by influencing speciation and extinction, and so "ecological limits" is really just one aspect of the traditional idea that ecology influences diversification. Ecological limits do not necessarily invalidate at-

tempts to use diversification rates to study patterns of species richness, and whether diversification rates are generally misleading about species richness patterns can be easily evaluated for any given study with a simple test (i.e., testing whether diversification rates of clades are correlated with their species richness). Whether ecological limits (a lack of increase in species richness over time) are present can only be shown directly by paleontological evidence, and the most relevant paleontological data (local richness over time) do not generally support the presence of ecological limits, although further study is clearly needed. The absence of a positive relationship between clade age and species richness is not direct evidence for strict ecological limits on richness within clades, and many of the analyses showing no age-diversity relationship were strongly biased to arrive at this conclusion. The idea that species richness within a group ceases to increase over time due to limited resources (the putative mechanistic explanation for ecological limits) is not necessarily a realistic expectation, but this is an area in need of further research.

There is ample evidence that both time and variation in diversification rates are major factors driving spatial species richness patterns, although the importance of time is only rarely tested (and should not be confused with "clade age," particularly for spatial richness patterns). Variation in diversification rates seems to be the major driver of two of Earth's most important diversity gradients: the well-known tropical versus temperate gradient and the less studied but more dramatic divide between terrestrial and marine environments. But there is evidence that the time-for-speciation effect influences both large and small-scale patterns in many groups, including different habitats within regions.

I outline one general approach for testing the causes of species richness patterns. This approach involves testing for ecological correlates of species richness patterns, identifying the evolutionary drivers of these correlations (time for speciation versus variation in diversification rates), and then determining how the ecological variables influence the evolutionary drivers.

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