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Species Diversity Is Dynamic and Unbounded at Local and Continental Scales*

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ABSTRACT: We argue that biotas at scales from local communities to entire continents are nearly always open to new species and that their diversities are far from any ecological limits. We show that the fossil, phylogenetic, and morphological evidence that has been used to suggest that ecological processes set limits to diversity in evolutionary time is weak and inconsistent. At the same time, ecological evidence from biological invasions, experiments, and diversity analyses strongly supports the openness of communities to new species. We urge evolutionary biologists to recognize that ecology has largely moved beyond simple notions of equilibrium at a carrying capacity and toward a richer view of communities as highly dynamic in space and time.

Keywords: diversity, saturation, community ecology, ecological limits.

Introduction: Against Ecological Limits

In this perspective, we will argue for a view of natural assemblages as open, unsaturated, and constantly in flux. We will draw from both ecological and evolutionary studies to provide abundant support for our view that ecological limits to diversity may not even exist and that, even if they do, assemblages are typically nowhere near them. Instead, diversity at any given place and time is determined by the dynamic interplay of immigration, extinction, and lineage diversification. Especially as we move from communities of interacting species to the diversities of entire continents, limits to diversity are likely irrelevant compared to the increasing influences of dispersal limitation, environmental heterogeneity, and long-term habitat change.

By contrast, our opponents argue that continental diversity is at or near ecological limits (Rabosky and Hurlbert 2015). To accept this proposition, it would be necessary to believe that ecological communities within continents consistently contain the maximum possible numbers of species dictated by resource availability. This means that competition is consistently strong, virtually all resources are used, vacant niches seldom exist, and the establishment of new species is generally possible only in conjunction with the extinction of resident species. The static diversity of these saturated communities, one would also have to believe, could be straightforwardly scaled up to entire continents, so that net evolutionary diversification as well as net immigration to continents will hover consistently around a mean of zero. We will show here that such a view is incompatible with both ecological and evolutionary studies of continental communities.

When our opponents view the incontrovertible evidence for open communities and dynamic diversity, they argue that this shows an equilibrium that is constantly changing, rather than a lack of meaningful ecological limits (Rabosky and Hurlbert 2015). We take issue with this view. Diversity equilibrium means that speciation (and immigration) equals extinction. These rates are only likely to equal one another when diversity dependence is strong—that is, when speciation slows and/or extinction accelerates with increasing diversity, possibly because ecological limits are being reached. Our opponents are effectively arguing that diversity is strongly governed by limits but that any contradictory evidence can be explained by invoking changes to the limits. We believe that this is not very parsimonious and that they can only save their argument by demonstrating the existence of strong equilibrial processes—evidence that is so far largely lacking.

We devote the first part of this article to examining evolutionary evidence that has been used to argue that observed diversity is controlled by ecological limits. We maintain that this argument, which includes both analyses of fossil diversity and phylogenetic comparative data, is consistently either flawed, ambiguous, or compatible with other explanations outside the scope of ecological limits. We then go on to examine ecological evidence from biological invasions, propagule addition experiments, and diversity analyses. We argue that these ecological data are also inconsistent

with the idea that local communities are commonly saturated. Instead, both evolutionary and ecological perspectives support our view of communities as complex, dynamic, open, and, typically, far from equilibrium.

Evolutionary Studies Show Little Evidence for Limits

A wide variety of evolutionary evidence has been used to argue in favor of limits to diversity. In this section, we argue that each of these lines of evidence is flawed, ambiguous, or consistent with other explanations outside the scope of ecological limits.

The Fossil Record Does Not Provide General Support for Ecological Limits

The most direct evidence we have for patterns of species richness through time comes from the fossil record. Time series of taxonomic diversity from fossils are most common for marine animals (e.g., Sepkoski 1979, 1981, 1984, 1997) but exist for other taxa as well (e.g., tetrapods; Benton et al. 2013). These time series provide great insights into patterns of diversity through time and lie at the core of the paleobiological revolution that shaped modern views of macroevolution (see Sepkoski and Ruse 2009 and references therein). Our intent here is not to provide a comprehensive review of the paleobiological literature on diversity limits, which is rich and interesting, but rather to illustrate the diversity of opinions and approaches and to show that the idea of diversity limits is highly contentious in paleontology.

Probably the most well-known example of a comprehensive analysis of diversity through time is Sepkoski's compilation of the diversity of marine animals through the past 500 million years (Sepkoski 1979, 1981, 1984, 1997). Sepkoski favored an interpretation of this diversity trajectory that is consistent with ecological limits. His interpretation relies on dividing the data into three "faunas" made up of taxa with similar patterns of diversity through time. One can then model the data with a three-phase model of logistic growth (Sepkoski 1981). However, there have been a number of criticisms of Sepkoski's interpretation, some of which focus on sampling and preservation biases. Indeed, attempts to correct these diversity curves for sampling can change patterns dramatically (Alroy et al. 2001, 2008). Using a database with such corrections, Alroy (2008) found little or no support for ecological limits or even any dependence of speciation or extinction rates on standing diversity (aside from recoveries following mass extinctions; see below). Other criticisms concern Sepkoski's methods for identifying ecological limits. For example, Stanley (2007) showed clearly that diversity curves simulated under Sepkoski's phased logistic model do not resemble real data

and argued that there is little sign of ecological limits to the macroevolutionary diversity of marine animals (see also similar arguments in Benton 1995; Courtillot and Gaudemer 1996; Benton and Emerson 2007; Erwin 2007, 2008).

One might expect the strongest evidence for ecological limits in studies of paleocommunities, which are groups of species that lived in a single place through a time interval on the order of hundreds to thousands of years (Bambach and Bennington 1996; Kowalewski and Bambach 2003). However, even these focused studies do not typically show patterns consistent with diversity limits or static equilibria (Bambach 1977; Powell and Kowalewski 2002; Bush and Bambach 2004). Benton and Emerson (2007) review a broad range of such studies to construct a strong argument against ecological limits and controls on macroevolutionary diversification.

Our interpretation of patterns in the fossil record differs from that of our opponents. We believe this difference relates at least in part to the standard of evidence required to demonstrate equilibrium. Our opponents suggest that any pattern that deviates from exponential increase or decrease is consistent with a "dynamic equilibrium" (Rabosky and Hurlbert 2015). However, it is insufficient to look at a plot of diversity through time and call it roughly constant without some sort of statistical support. For example, figure 1 shows two plots used as examples of diversity equilibria in a recent review by Rabosky (2013). Verbal descriptions like "largely equilibrial" applied to the strongly varying patterns in figure 1 seem, to us, inaccurate and insufficient. Diversity equilibrium implies that specific mechanisms are at work, and positive evidence for these mechanisms and their outcomes is essential (e.g., Alroy 2008). Although one can find occasional statistical support for equilibrium, we argue that, on the whole, such evidence is largely lacking.

When reviewing the paleontological literature in light of this debate, it is critical to understand the relationship between diversity-dependent diversification and ecological limits. For ecological carrying capacities to set limits to diversity, there must be diversity dependence, specifically a tendency for per-lineage speciation rates to decrease and/or extinction rates to increase as a function of standing diversity. However, such diversity-dependent patterns can also arise from many processes unrelated to ecological limits, such as differences in population size and/or range size, or the dynamics of speciation mode (reviewed in Moen and Morlon 2014). Moreover, diversity dependence only implies an upper limit to diversity when it is strong enough to actually stop diversification as opposed to just slowing it down (Benton and Emerson 2007; Foote 2010; Cornell 2013). Therefore, although net diversification rates are sometimes elevated during the recovery periods following mass extinctions (e.g., Kirchner and Weil 2000; Krug and Jablonski 2012), and although a number of studies have re-
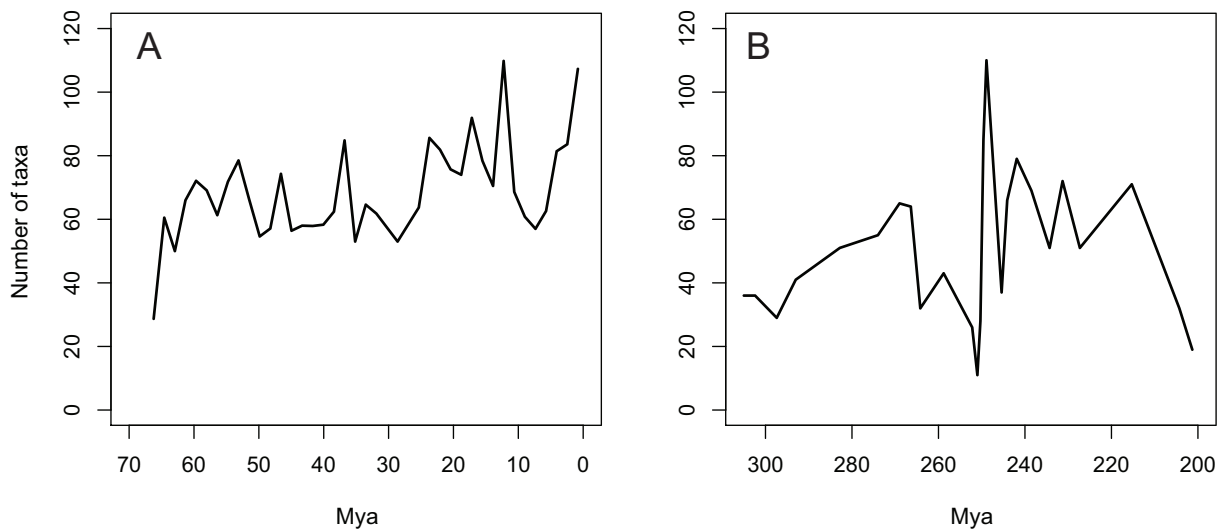
Figure 1: Plots of taxonomic diversity through time, used as evidence for equilibrial dynamics by Rabosky (2013). *A*, Species richness through time in North American mammals (Alroy 2009). *B*, Generic richness through time in ammonites (Brayard et al. 2009).

ported a slight slowing of diversification as diversity increases (i.e., diversity continues to increase but at a less than exponential rate; e.g., Miller and Sepkoski 1988; Benton and Emerson 2007; Cornell 2013), this evidence for diversity-dependent diversification is less than sufficient to show that diversity is governed by ecological limits.

We believe it is incorrect to characterize paleobiological research as giving widespread evidence for ecological limits. In addition to the arguments above, we have three particular criticisms of the way that paleobiology has been invoked by neontologists to support theories of ecological limits. First, statistical evidence is required to demonstrate that a time series of fossil diversity is actually at some equilibrium (e.g., Alroy et al. 2008). Too often, plots of diversity through time are interpreted in a completely ad hoc way, such that even patterns with huge variation in species number through time are argued to be undergoing "stationary dynamics" or a "dynamic equilibrium" or even as moving between different "plateaus" of diversity equilibria, all in the absence of any quantitative analysis. Second, patterns of fossil diversity through time show a wide variety of patterns; they can be flat but also can be increasing, decreasing, or any other pattern (Benton and Emerson 2007). To make any general conclusions about ecological limits from such data, one must either show a preponderance of equilibrium patterns or be able to reliably predict when and where one might see a saturated pattern. Finally, fossil diversity patterns are almost never at the species level; instead, such plots almost always show the diversity of higher-level taxa (genera, families, etc.) through time. Such patterns do not connect directly to ideas of saturation at the species level

without either a model connecting these higher-level taxa to species (e.g., Foote 2012) or a compelling argument about ecological saturation at higher taxonomic levels.

In short, although the topic of ecological limits is clearly a central issue in paleobiology, it is far from any resolution. Fossil data do not provide general support for the idea that there are ecological limits to diversity.

"Slowdowns" from Phylogenetic Data Provide No Evidence for Ecological Limits

Phylogenetic trees with branch lengths can be used to infer patterns of diversification through time (Nee 2001) and are often a key component of recent arguments in favor of diversity limits (Rabosky 2009b, 2013). Some of this discussion has centered on age-diversity relationships (Rabosky 2009a; Wiens 2011; Rabosky et al. 2012). One can prune a set of clades from a phylogenetic tree, measure their ages (either crown or stem) and current-day diversities, and test for a relationship between age and diversity. A common interpretation of these results is that a lack of a relationship between age and diversity is evidence for ecological limits (Rabosky 2009a, 2009b; Rabosky et al. 2012). However, and as already conceded by our opponents in their companion article (Rabosky and Hurlbert 2015), this pattern is far from ubiquitous in real data and is compatible with other explanations (see also further discussion in Wiens 2011 and Stadler et al. 2014). Furthermore, one should be reluctant to form strong biological conclusions about the presence of a process from the absence of a pattern, in this case, the lack of a correlation between age and diversity.

The increasing emphasis on ecological limits on macroevolution has partly been inspired by a pervasive pattern of slowdowns in the rate of lineage accumulation in phylogenetic trees. The most common way to show this pattern is through lineage-through-time plots, which are expected to show a decrease in slope toward the present day if ecological limits dominate. A range of statistical methods have been invented to detect such slowdowns, with the most common being Pybus and Harvey's (2000) gamma statistic. More recent approaches rely on fitting models with diversity dependence, time dependence, or ecological limits to phylogenetic branching times (Rabosky and Lovette 2008; Potts et al. 2010; Etienne et al. 2011; Etienne and Haegeman 2012; reviewed in Pyron and Burbrink 2013). Both individual studies and meta-analyses have shown that such models often provide a better fit than alternatives for phylogenetic trees of a wide range of organisms (e.g., Rüber and Zardoya 2005; McPeek 2008; Phillimore and Price 2008; Moen and Morlon 2014; but see Derryberry et al. 2011 and Day et al. 2013 for two counterexamples).

However, there are some reasons to be skeptical of the connection between this observed pattern of slowdowns in lineage-through-time plots and ecological limits (Moen and Morlon 2014). First, slowdowns may be a statistical artifact of the way phylogenetic branch lengths are estimated. Model misspecification—in particular, the use of models that do not adequately capture the dynamics of molecular evolution—can lead to biased inferences of branch lengths (Revell et al. 2005). Typically, branch lengths are underestimated when inadequate models are applied, and this problem becomes more severe for older compared to younger branches in the tree. This leads to an artifactual "slowdown" signal even in trees generated under pure-birth models with no changes in rate through time. Model misspecification may also be a problem in cases where birth- and/or death rates vary across clades in a tree (e.g., Alfaro et al. 2009).

Second, slowdowns are more likely to reflect taxon sampling than biology (Cusimano and Renner 2010; Brock et al. 2011). Even random incomplete sampling tends to leave out species that are connected to relatively young nodes in a phylogenetic tree, leading to patterns that mimic a slowdown. This potential issue was identified by Pybus and Harvey in their foundational article (2000), and they suggest a randomization test that can correct for incomplete sampling: one simulates phylogenetic trees with the same sampling fraction as the real data and compares the resulting slowdown statistics (this is called the Monte Carlo constant rates [MCCR] test). The MCCR test is a viable solution as long as we know how many species are unsampled, and the included lineages represent a random sample of all species in the clade. However, both of these assumptions are probably often invalid. For example, we may not know for sure how many extant species there are in our focal group.

Perhaps more importantly, the MCCR test assumes that we have randomly sampled species in the focal clade; however, nonrandom sampling, which is likely extremely common (and, in fact, is often a goal of phylogenetic systematic studies that seek to uncover the deepest relationships in a clade), can lead to biased results (Cusimano and Renner 2010; Brock et al. 2011).

Third, there are serious artifacts that come from defining species for phylogenetic analyses of slowdowns. If speciation takes time—an undoubtable fact—then extant groups will be a mix of incipient and full species (Rosindell et al. 2010). Systematists wishing to be taxonomically conservative tend to prune out lineages that are not full species prior to comparative analyses. However, this pruning of the youngest nodes in phylogenetic trees is bound to lead to patterns of "slowdowns" even when the process of lineage diversification is constant through time. This idea is perhaps best captured by models of protracted speciation, which can mimic slowdowns as seen in phylogenetic trees even without invoking ecological limits to diversity (Rosindell et al. 2010; Etienne and Rosindell 2012).

Finally, lineages in these slowdown plots are only rarely species from a community that might be thought to have ecological limits on richness. Instead, most phylogenetic trees include species from a range of areas, many of which do not interact with one another (Wiens 2011; Pinto-Sanchez et al. 2014). Verbal models of full niches and saturated niche space make little sense when species live in entirely different parts of the world. In fact, it seems to us that slowdowns in such trees, which include taxa from widespread areas that have not been in contact with one another for millions of years, argues against any explanation for these patterns that relies on ecological interactions. Instead, one should ideally use comparative data to simultaneously infer historical community composition and test for community saturation (e.g., Pinto-Sanchez et al. 2014).

Taken as a whole, these arguments cast serious doubt on the idea that phylogenetic trees give strong and consistent support for ecological limits (Moen and Morlon 2014). Our opponents may have already conceded this point, but evidence from phylogenetic trees continues to be used in many articles to support arguments in favor of ecological limits and saturated diversity. The fact that the slowdown pattern is so persistent, seemingly regardless of any biological and geographical differences across groups, argues more in favor of this pattern being a statistical artifact than revealing any biological phenomenon.

Adaptive Radiations Show No Signs of Slowing through Time

Adaptive radiations should be the ultimate test case for ecological limits. The ecological theory of adaptive radia-

tion posits that adaptive radiations are driven by ecological opportunity, which can come from a key innovation, mass extinction, or dispersal into a new area (Simpson 1944; Schluter 2000; Yoder et al. 2010). If ecological opportunity triggers an adaptive radiation, one might also expect radiations to slow down or stop as that opportunity is used up (Harmon et al. 2010; Yoder et al. 2010). More specifically, if one accepts arguments about ecological limits, one might posit that slowdowns should be most visible in species' traits, which actually mediate competition and niche overlap, rather than in the number of species, which might be only loosely connected to "niche packing." However, tests for slowdowns in trait evolution have been mixed to negative—slowdowns have been found in some clades but seem to be rare overall and are not associated with clades typically described as "adaptive radiations" like anoles or Darwin's finches (Harmon et al. 2010; but see Slater and Pennell 2013 for a methodological comment on that study pointing out that this test can have low power). The few exceptions tend to be found on islands rather than continents (e.g., Mahler et al. 2010).

Overall, although there is some evidence for a role of ecological opportunity in the beginnings of adaptive radiations, there is little evidence that this opportunity ever gets "used up" as continents near their ecological limits.

Ecological Evidence Argues Against Community Saturation

At the heart of the notion of limits to continental diversity are the ecological concepts of carrying capacity, limiting similarity, and community equilibrium. Yet as we argue in this section, modern ecological evidence suggests that stable communities governed by fixed carrying capacities are more of a cartoon than a reality. Instead, we more commonly observe transience, invasibility, and weak or indeterminate interactions among species in natural communities. Even at small spatial scales, a community's approach to equilibrium is very unlikely to keep pace with disturbance, directional habitat change, or other alterations. In this section, we explore three lines of ecological evidence that cast doubt on ideas of limits to diversity: energy-richness correlations, biological invasions, and relationships between local and regional species richness.

Energy-Richness Correlations Are Unconvincing

Continental-scale species richness in terrestrial plants and animals is generally strongly positively correlated with variables related to primary productivity, including solar radiation, rainfall, actual evapotranspiration, and remotely sensed indexes (Hawkins et al. 2003). Some authors have used this evidence to argue that diversity can be set by an energetic carrying capacity (Hurlbert and Stegen 2014), but there are multiple reasons to question this interpretation. First, diversity shows no consistent pattern with primary productivity in local communities (e.g., Mittelbach et al. 2001; Adler et al. 2011), precisely the scale at which species compete and the influence of carrying capacity ought to be most detectable. Second, carrying capacity as measured by the numbers of individuals has not succeeded in explaining the link between productivity and diversity, that is, there is little evidence for the "more individuals hypothesis" (Currie et al. 2004; Hurlbert and Jetz 2010). Third, there are at least two other explanations for the terrestrial diversity-productivity relationship. One is the "tolerance" or "niche conservatism" hypothesis, proposing that regional species richness is higher in climates resembling the warm and humid conditions of the Eocene because many lineages diversified at that time and have retained an intolerance of cold and/or arid conditions (Wiens and Donoghue 2004). Another is the "faster diversification" hypothesis, proposing that net diversification rates are higher in benign climates (Mittelbach et al. 2007). One particularly revealing test of energetic carrying capacity comes from the deep oceans, where productivity is decoupled from temperature and rainfall. Benthic foraminiferan diversity in the deep sea is positively related to temperature, quite similarly to the "energy-richness" relationships that are observed on land, but diversity is not related to productivity as measured by a biologically based index of organic carbon flux (Hunt et al. 2005).

Species richness is of course correlated with innumerable environmental gradients besides productivity, including soil pH, salinity, habitat age, habitat isolation, and elevation. Rather than conceiving each of these influences as representing a fixed carrying capacity for species, it is more reasonable to interpret them as influences on the (diversity-independent) rates of species loss and gain through immigration, speciation, and extinction. In fact, for compelling evidence that environmental correlates of richness do not equate to environmental limits to richness, we need only turn to biological invasions.

Invasions Continually Increase Diversity

Biological invasion—an unintentional and ongoing experiment at the largest possible spatial scale—has shown decisively that biotas are open to new species at scales from communities to continents. We know, for example, that terrestrial plant richness at the regional scale in California is correlated with primary productivity, which in turn is governed by a latitudinal gradient in rainfall (Harrison et al. 2006). Yet we also know that in the past two centuries, the Californian flora gained more than 1,000 naturalized exotic species (or 20% of its current size) while losing

only 28 native species (Sax et al. 2002). This pattern is consistent with the finding that biotic interchange and faunal mixing can lead to increased diversity over very long timescales (reviewed in Vermeij 1991). Species gains through invasion tend to be highest in the most species-rich communities, opposite to the pattern predicted under saturation (Stohlgren et al. 2008).

Openness of communities to new species through recent invasions is seen worldwide, involving animals and plants in marine, freshwater, and terrestrial habitats and at a wide range of spatial scales. In fact, a consortium of leading invasion biologists concluded that the most significant lesson for ecology and evolution to emerge from the decades of work in their field is that "ecological systems rarely show evidence of being saturated with species" (Sax et al. 2007, p. 466). Of the very few examples in which competition with invasive species has led to native species extinctions, they conclude, nearly all have taken place at scales of 1 m^2 or less. Underlining this point still further, their second major conclusion is that "competition, unlike predation, seldom causes global extinction" (Sax et al. 2007, p. 466). Competitors even appear to coexist and elevate diversity following the massive natural invasions that occur during natural biotic interchanges (Vermeij 1991; Tilman 2011). Experimental "invasions" of plant communities with propagules of other species also support community openness. Seed addition significantly increased plant community richness in a meta-analysis of 62 studies, and this increase was seen even in undisturbed conditions, although disturbance increased the effect size (Myers and Harms 2009).

Two global meta-analyses cited by our opponents recently concluded that, despite the multitude of human impacts causing global and local extinctions, diversity at scales less than global shows no consistent tendency to decline (Vellend et al. 2013; Dornelas et al. 2014). While neither study found consistent increases in community diversity across all regions and taxa, Dornelas et al. (2014) did conclude that invasions have driven general increases of diversity in terrestrial plants and in the temperate zone (where invasions are more common and recent human-caused extinctions less common than in the tropics). Rather than even hinting at the possibility of stable or equilibrial diversity, these studies emphasized that "increases [are] just as likely as decreases" (Vellend et al. 2013, p. 19548) because of "the complexity and heterogeneity of outcomes at different locations and scales" (Dornelas et al. 2014, p. 299), a view of diversity that is entirely consistent with our arguments.

Most Communities Show Unsaturated Patterns of Diversity

Local-regional-richness (LRR) relationships are another widespread form of evidence against saturated communities. When the species richness of local communities is re-gressed against the species richness of their surrounding regions, the most common relationship is positive, consistent with the diversity of local communities being strongly influenced by the availability of species from the region (reviewed in Cornell and Harrison 2014). These LRR analyses have been criticized for being tautological (is it surprising to find correlations between the same variable at two scales?) and for being explainable by dynamic interactions among local communities rather than by top-down regional influences (see Harrison and Cornell 2008). However, the best LRR analyses are immune to these criticisms because they deal with very different regional and local scales and because they address causes of variation in regional richness that are clearly not local. For example, the numbers of cynipid gall wasps coexisting on individual oak trees are determined by the number of wasps found on that oak species as a whole, which in turn depends on the geographic range of the oak species (Cornell 1985). Numbers of coral species in 10-m transects are determined by regional species numbers found in broad swaths of the western Pacific Ocean varying in distance from the Indonesian coral hot spot (Karlson et al. 2004). These results are difficult or impossible to explain except by regional control over local community diversity.

Our opponents point out that there must be a theoretical higher limit to diversity that must exist at any point in time: the situation where every individual is a different species (S_{MAX}, in their terminology; Rabosky and Hurlbert 2015). However, all natural species abundance distributions share a common shape that shows no evidence of approaching this hypothetical scenario (McGill et al. 2007). In other words, the hypothetical idea of a "saturated" community, in which every individual is a different species, is irrelevant to the argument at hand. An equilibrium might also seem inevitable from plots of speciation and extinction rates versus standing diversity (Rabosky and Hurlbert 2015, fig. 1). This idea follows MacArthur and Wilson (1967); however, we note that in island biogeography, this equilibrium is determined by the assumption of a fixed mainland species pool. In the simplest version of the equilibrium theory of island biogeography, immigration to islands goes down with island diversity simply because the mainland pool is exhausted. At the continental scale we are considering, this "species pool" does not exist, and in fact, the relationship between species diversity and speciation (and extinction) rates remains under debate in almost all cases.

In summary, ecological evidence overwhelmingly supports the openness of communities to new species, even at the small spatial scales where species interact and the influences of competition and resource supply should be strongest. At the scale of entire continents, where the vast majority of species pairs never even co-occur and where

the slowness of dispersal relative to the rate of environmental change can delay or prevent the attainment of equilibrium (e.g., Jackson and Overpeck 2000; Svenning and Skov 2004), there is little reason to believe that the addition of new species is ever inhibited by the richness of resident species.

Modern Theory Does Not Support Limits to Species Richness

In our view, the current debate on limits to continental species richness contains echoes of bygone mid-twentieth-century ecological controversies, including the population regulation debate of the 1950s–1960s (see Turchin 1999) and the competition and community structure debate of the 1980s (see Schoener 1983). Both of these pitted theoretically minded workers fond of simple models against hard-headed empiricists insistent on pointing out flawed model assumptions, weak evidence, and the far greater complexity of nature. The outcome of this long dialogue, we believe, has been the development of a richly nuanced theory of populations and communities that embraces complexity in the form of transient (e.g., Hastings 2004), nonequilibrial (e.g., Rohde 2005), and high-dimensional (e.g., Clark et al. 2007) dynamics. Simple local determinism is strongly questioned (Ricklefs 2008), and scaling up from local processes to regional dynamics is considered a major theoretical challenge (Chesson et al. 2005). Standards for supporting theory with evidence also have risen dramatically. Thus, while understanding large-scale diversity requires merging insights from ecology and evolutionary biology, we would caution against overly simplistic and outdated ideas about equilibria and carrying capacity.

Conclusions: Open Communities and Dynamic Diversity

At local ecological scales, theory and evidence have identified several conditions that tend to make communities "unsaturated" or open to new species (see review in Cornell and Harrison 2014 and references therein). Disturbance, keystone predation, resource pulses, or other habitat changes may happen frequently or rapidly enough to prevent communities from reaching competitive equilibria at which niche space is fully occupied. Dispersal limitation, enhanced by large spatial scales and by natural barriers, contributes to slowing the attainment of competitive equilibria. Recently, it has been argued that when species are relatively similar in fitness, they can coexist in a quasineutral fashion for long periods of time even if their niches are identical (e.g., Zhou and Zhang 2008). Empirical studies also find little evidence for saturation in communities containing many rare, transient, and/or weakly

interacting species, as is often the case in heterogeneous habitats. Indeed, the hallmarks of saturated communities, such as negative correlations between diversity and abundance or between diversity and niche breadth, are seldom found.

At continental scales, therefore, it is also possible to create a comprehensive theory of diversity dynamics without ecological limits. We view continental biotas as temporary assemblages of species that are typically out of equilibrium and in constant flux due to continually changing environments (Jackson and Overpeck 2000) and the ecological and evolutionary dynamics of species. Species interact with one another and with their abiotic environment, leading to dramatic differences in diversification rates both across clades and through time. In this view, equilibrium dynamics are irrelevant; either ecological limits do not exist or communities are only rarely and transiently affected by them. Diversification rates might be slightly or temporarily influenced by standing diversity but are not strongly or consistently affected by ecological limits.

We and our opponents concluded our debate by asking one another, What would it take to make you change your mind? For our part, we would believe that continental diversity is governed by ecological limits if (1) fossil and phylogenetic evidence showed that rates of net diversification are so strongly negatively correlated with standing diversity that diversity cannot increase past a certain point; (2) comparative data showed a clear pattern of slowdowns in both speciation and trait evolution as niche space in communities becomes filled by species; and (3) ecological evidence showed a preponderance of natural communities that are stable and uninvasible or in which invasions tend to lead to equal numbers of resident species extinctions. For now, we believe that the great preponderance of evidence points toward continental diversity being nowhere near any limits set by resources and competition.

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"Vast numbers of Corixidae were living in the water"—G. E. Hutchinson (*The American Naturalist*, 1959, 93:145–159). Artwork by Simone Des Roches.