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Ecological and Evolutionary Drivers of Geographic Variation in Species Diversity

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Annu. Rev. Ecol. Evol. Syst. 2015. 46:369–92

First published online as a Review in Advance on October 16, 2015

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-112414-054102

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Keywords

biotic interactions, climate stability, evolutionary speed, latitudinal gradient, time-integrated area, tropical niche conservatism

Abstract

Recent studies have generated an explosion of phylogenetic and biogeographic data and have provided new tools to investigate the processes driving large-scale gradients in species diversity. Fossils and phylogenetic studies of plants and animals demonstrate that tropical regions are the source for almost all groups of organisms, and these groups are composed of a mixture of ancient and recently derived lineages. These findings are consistent with the hypothesis that the large extent of tropical environments during the past 10–50 million years, together with greater climatic stability, has promoted speciation and reduced extinction rates. Energy availability appears to only indirectly contribute to global patterns of species diversity, especially considering how some marine diversity gradients can be completely decoupled from temperature and productivity gradients. Instead, climate stability and time-integrated area together determine the baselines of both terrestrial and marine global diversity patterns. Biotic interactions likely augment diversification and coexistence in the tropics.

1. INTRODUCTION

From humble beginnings more than 3 billion years ago, living organisms have colonized and transformed almost all marine and terrestrial environments on Earth and, in the process, evolved myriad forms, physiologies, and life histories. Yet such diversity is not evenly distributed around the globe and observers have wondered for centuries about the causes of striking diversity patterns such as the latitudinal diversity gradient, elevational gradients on land, and bathymetric gradients in the ocean. Elucidating the processes by which diversity arises has been a central occupation of biologists since Darwin and Wallace. A complete understanding of diversity also entails investigating why some species survive and others die out, which involves ecology. Thus, research into lineage divergence and persistence (evolutionary biology) as well as organismal survival and coexistence (ecology) must be integrated to understand why certain areas of the planet harbor larger numbers of taxa than other areas.

The past decade or so has seen an explosion of new data on species distributions and fine-scale maps of climatic and environmental variables plus enormous advances in reconstructing the tree of life. Integrations of biogeographic and phylogenetic data have given new resolution to the distribution patterns of species diversity at the global scale as well as the phylogenetic relationships of organisms at a variety of taxonomic scales. Examining the mechanisms underlying patterns of species diversity is critical, especially as humans affect major modifications of the environment (Newbold et al. 2015). Humans are reducing habitat areas for most of the world's species while global temperature and precipitation patterns are also changing, and these variables are at the center of many theories to explain the origin and maintenance of species diversity. Although the primary causes underlying gradients in species diversity at global scales are often referred to as unexplained—I argue here that we know an enormous amount about the most important drivers of geographic variation of species diversity. A new synthesis is emerging that acknowledges the importance of historical factors such as evolution and biogeography as well as contemporary factors such as climatic and environmental variables in determining species' geographic ranges and the accumulation of species within regions. Furthermore, we now know much more detail about the role of environmental thresholds that limit species from dispersing into new adaptive zones and how often adaptation to these environments occurs within lineages.

In this review, I first briefly examine the geographic and taxonomic scales at which the patterns of geographic variation in species diversity can most profitably be evaluated. Although I am interested in understanding the general causes of geographic variation in diversity across the globe, I focus much of this review on the latitudinal diversity gradient, because this is the predominant and best-studied biodiversity pattern on Earth. I next summarize and review hypotheses that are the most relevant to explaining variation in species diversity at the regional scale. I then evaluate these hypotheses and summarize current theories to explain diversity gradients. Finally, I conclude with recommendations for the next wave of diversity scientists.

2. DIVERSITY AT THE REGIONAL SCALE

One of the fundamental insights of the past 25 years is that regional diversity and local diversity have a hierarchical relationship (Ricklefs 1987, 2004; Webb et al. 2002). Examining the drivers of diversity gradients requires a large-scale approach, because ultimately, we are interested in the factors that have led to the diversification of the resident biota of a species pool, which in turn have influenced the numbers (and identities) of species in local communities. For these reasons, this review focuses on the regional scale.

In order to test the mechanisms driving regional diversity, one needs to define the world's regions and quantify the diversity within them. Ideally, these regions should represent independent replicates and thus not overlap too much in species composition (Jetz & Fine 2012). Comprehensive lists of the diversity and phylogenetic relationships of the resident biota must be available for these regions as well as accurate region-wide data on the various drivers hypothesized to drive diversity differences (i.e., area, productivity, temperature, biotic interactions, and climate stability).

Thus, tests of the drivers of regional diversification require the delineation of regions with biologically meaningful boundaries that correspond with the physiological and biotically enforced thresholds that enforce concordant geographic range limits for regional species assemblages. Biomes are a reasonable starting point to describe the boundaries of regions, because they are defined by climate variables that correlate with significant changes in vegetation type (Woodward 1987). Jetz & Fine (2012) used biome maps to delineate 32 vertebrate bioregions (bioregions is a term used to describe biomes within continents or realms). They further investigated the accuracy of these putative bioregions to accurately describe the evolutionary arenas of vertebrates by calculating overlap in species composition. Studies using β -diversity measures of different clades of vertebrates have yielded different numbers of independent regions, generally between 11 and 38 (not including islands) (Kreft & Jetz 2010, Holt et al. 2013). Similar approaches for marine fauna have delineated 68 marine provinces (Spalding et al. 2007). Putative bioregions can be compared at different scales to serve as a type of sensitivity analysis (Kisel & Barraclough 2010, Belanger et al. 2012). Using phylogenetic information to delimit bioregions may also provide an indication of how well putative bioregions represent evolutionary arenas of in situ evolution (Holt et al. 2013).

The boundaries delimiting bioregions result from processes affecting dispersal, survival, or gene flow (Donoghue & Edwards 2014). First, a taxon may never have dispersed to a second bioregion and/or could belong to a clade that has low dispersal capability. Second, the taxon could have some physiological constraint preventing survival or reproduction in the new bioregion (e.g., the taxon has no frost tolerance). Third, the taxon may disperse to a new bioregion, survive and reproduce, but then, due to evolutionary trade-offs, gene flow between populations spanning a bioregional boundary could quickly become disrupted across the boundary, resulting in lineage divergence.

What are the evolutionary trade-offs that promote speciation when populations of a taxon span bioregional boundaries? For plants, frost tolerance is required to survive poleward from the frost line, and plants without frost tolerance are quickly eliminated during freezing events, even if freezing does not occur annually. Frost tolerance represents a major energy investment that could otherwise be used for growth or reproduction (Loehle 1998). Thus, plants with frost tolerance cannot grow as fast as those without frost tolerance and are thought to be out-competed in frost-free areas (MacArthur 1972). This pattern of poleward range limits caused by physiological constraints and equatorial range limits enforced by biotic factors appears to be generally true for plants and animals and has been termed the Dobzhansky–MacArthur phenomenon (Brown 2014). Indeed, there are very few species of trees that have geographic ranges on both sides of the frost line (Fine 2001). Similar trade-offs likely occur in animals, but because they are more mobile and can migrate or become dormant, the trade-offs may be less easy to identify. Nevertheless, although there are many famous exceptions, the vertebrate and invertebrate fauna almost completely turns over between tropical and extratropical terrestrial bioregions (Hawkins 2010, Jetz & Fine 2012). Moreover, many animals may be tracking plant species distributions, especially those that have any sort of host–specialist relationship (Ehrlich & Raven 1964, Condamine et al. 2012).

Bringing phylogenies to bear on the question of how often lineages shift across biome boundaries has led to a strong consensus that niche conservatism at the biome scale is pervasive. Most lineages from major groups of organisms such as birds, amphibians, angiosperms, and many marine

invertebrates all originated in the tropics (Wiens & Donoghue 2004, Jablonski et al. 2006, Wiens et al. 2010, Kerkhoff et al. 2014). These studies have confirmed that tropical regions are the source for most diversity. Whereas many tropical marine taxa have ranged into the temperate zone (Jablonski et al. 2006), for terrestrial lineages, physiological tolerances to withstand cold or freezing temperatures and dry conditions have evolved relatively infrequently (Wiens et al. 2010). This point, that lineages only rarely cross biome boundaries, provides the critical justification for comparing the properties of bioregions in an investigation of large-scale drivers of species diversity. In other words, for lineages that only rarely cross biome boundaries, most speciation events must be occurring inside the borders of bioregions. For lineages that exhibit little biome conservatism (i.e., microbes, Hanson et al. 2012), correlating properties of a bioregion with species richness or diversification rate is not justified—for these groups it would be most important to understand the frequencies of transition across biomes, the dispersal rates of lineages, and the sizes of the transition zones or boundaries between biomes (Donoghue & Edwards 2014).

3. HYPOTHESIZED DRIVERS OF SPECIATION AND EXTINCTION OF RESIDENT BIOTA WITHIN BIOREGIONS

In 1966, Eric Pianka wrote the first review paper on large-scale diversity gradients and reviewed six major hypotheses to explain the latitudinal diversity gradient. Since then, several reviews have added new hypotheses to this list (Rohde 1992, Willig et al. 2003, Mittelbach et al. 2007). Complicating matters, some of these hypotheses often involve the same drivers, namely geographic area, available energy, climate stability, and biotic interactions, and generate similar predictions about diversity and diversification rate because most of the hypothesized drivers covary with latitude (**Table 1**). In the spirit of emphasizing common ground, as well as trying to make order out of chaos, I have combined several older hypotheses into broader explanations and excluded from the discussion those that have been rejected with sufficient justification (**Table 1**).

Schemske (2002) divided the potential drivers of the latitudinal diversity gradient by their potential influence on the different phases of lineage divergence and persistence. Although Schemske (2002) focused solely on allopatric speciation when discussing lineage divergence, I extend this approach to also incorporate parapatric and sympatric speciation (including habitat specialization and trophic specialization) into the same framework. For some clades of organisms, nonallopatric speciation may be an especially important mechanism for lineage divergence (Schluter 2001). Lineage divergence can be divided into three sequences (**Figure 1**): (*a*) Populations encounter and become subdivided by a geographic barrier, novel habitat, or new trophic resource; (*b*) reproductive isolation evolves as a result of either natural selection or genetic drift, such that the two (or more) diverging lineages eventually become reproductively incompatible; and (*c*) populations persist, resulting in a net gain of taxa in the region. In the case of parapatric or sympatric speciation, this phase occurs more rapidly across strong selection gradients, because intermediate phenotypes are not favored and are out-competed by both parental types (Endler 1977).

In this review, I address five combined hypotheses, which for the most part are not mutually exclusive but instead form a nested hierarchy with more complex hypotheses adding additional predictions to the simpler hypotheses. I organize these hypotheses by their large-scale drivers: area, energy, time, climate stability, temperature, and biotic interactions (**Table 1**).

3.1. Area, Energy, and Time

At the regional scale, area is thought to influence speciation through its effect on population size with the assumption that larger areas can support larger numbers of individuals (Rosenzweig 1995, Kisel et al. 2011). Population sizes, in turn, should be positively related to geographic range size

Table 1 Hypothesized drivers for large-scale gradients, their mechanistic bases, and their predictions about speciation, extinction, and specialization in tropical versus temperate bioregions

Hypothesis (citation)	Status in this review (citation if rejected)	Mechanism	Predict higher speciation rates in tropics?	Predict lower extinction rates in tropics?	Predict higher specialization rates in tropics?
Geographic area (W, R, M)	Included in area/energy/time hypothesis	Larger regions should have larger average population sizes, which should have higher speciation and/or lower extinction rates. Because speciation and extinction take time, area and time must be considered together.	Yes	Yes	No prediction
Tropical conservatism (M)	Included in area/energy/time hypothesis	See above	Yes	Yes	No prediction
Out of the tropics (M)	Included in area/energy/time hypothesis	See above	Yes	Yes	No prediction
Available energy/productivity (W, R, P)	Included in area/energy/time hypothesis and ecological limits hypothesis	More energy should increase population sizes. This should increase speciation and reduce extinction rates (see above), as well as allow for a greater carrying capacity for species (see below)	Yes	Yes	Yes
Competition/niche width (R)	Included in ecological limits hypothesis	Regions with more available energy are able to support a higher equilibrium diversity, enforced by biotic interactions in a zero-sum relationship among community abundances within regions.	Yes	Yes	Yes
Climate stability/ambient energy (R, W)	Included in climate stability hypothesis	Regions with more climatic stability have lower extinction rates; climate stability promotes narrow physiological tolerances and specialization in general, increasing speciation rates, and isolates formed by allopatry are more likely to persist	Yes	Yes	Yes
Rapaport's rescue/narrow physiological tolerance (W, M)	Included in climate stability hypothesis	See above	Yes	Yes	Yes
Parapatric/sympatric speciation (M)	Included in climate stability hypothesis	See above	Yes	Yes	Yes
Spatial heterogeneity (P)	Included in climate stability hypothesis	See above	Yes	Yes	Yes
Evolutionary speed (W, R, M)	Included in evolutionary speed hypothesis	Regions with more temperature (kinetic energy) harbor organisms with faster metabolic rates and generation times, speeding up natural selection and speciation rates	Yes	No prediction	Yes

(Continued)

Table 1 (Continued)

Hypothesis (citation)	Status in this review (citation if rejected)	Mechanism	Predict higher speciation rates in tropics?	Predict lower extinction rates in tropics?	Predict higher specialization rates in tropics?
Competition/ predation (P)	Included in biotic interactions hypothesis	Regions with stronger biotic interactions could have increased speciation rates due to positive feedback on coevolutionary rates across a geographic mosaic and could have reduced extinction rates due to increased competition driving finer niche specialization or increased predation causing less competition and more coexistence.	Yes	Yes	Yes
Biotic interactions (M)	Included in biotic interactions hypothesis	See above	Yes	Yes	Yes
Genetic drift (R, M)	Rejected (R, M)	Genetic drift of small populations increase speciation probabilities in diverse systems	Yes	No prediction	No prediction
Geometric constraints/ mid-domain (W)	Rejected (C)	Large-scale gradients occur randomly	No prediction	No prediction	No prediction
Time (R, M)	Rejected (R, M)	More time to diversify	No prediction	No prediction	No prediction

Abbreviations: C, Currie & Kerr 2008; M, Mittelbach et al. 2007; P, Pianka 1966; R, Rohde 1992; W, Willig et al. 2003.

and genetic diversity (**Figure 1**). Geographic range size is thought to be related to the probability for allopatric speciation to occur, given that small-ranged species may not have the opportunity to be subdivided by a barrier within regions. Nevertheless, large-ranged species may also have smaller likelihoods of becoming subdivided if their ranges are large enough to surround a barrier, leading to the rather unsatisfying prediction that species with intermediate-sized ranges should have the highest speciation rates (Rosenzweig 1995, Chown & Gaston 2000). Larger bioregions should also contain more environmental heterogeneity than smaller bioregions (Kisel et al. 2011). Bioregions that have experienced tectonic activity like mountain uplift have increased opportunity for barriers and environmental gradients to promote speciation. For example, the uplift of the Andes coincides with the timing of diversification for many South American montane and lowland lineages (Hoorn et al. 2010, Antonelli & Sanmartín 2011). Finally, greater genetic diversity of larger population sizes translates into greater phenotypic variability and increases the likelihood that populations encountering environmental heterogeneity can survive in different habitats, which is a prerequisite for parapatric speciation (Nuismer et al. 2012).

The relationship between geographic range size and extinction probabilities is more straightforward, as small bioregions have smaller-ranged species on average; these species should have higher extinction risk due to catastrophic events (Lande 1993, Rosenzweig 1995, Chown & Gaston 2000). In addition, small populations with low genetic diversity can experience extinction risks

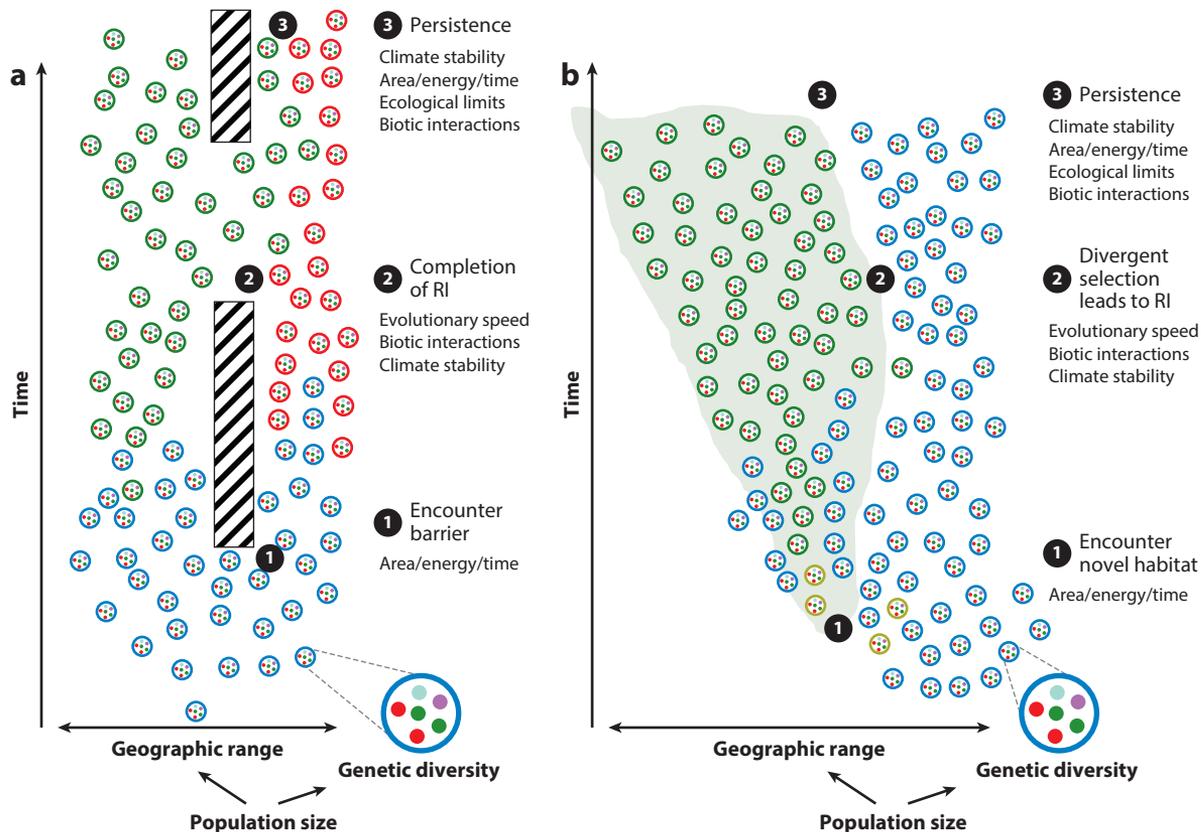


Figure 1

(a) This schematic shows how population size, through its effects on geographic range size and genetic diversity, influences the probability of allopatric speciation. Color changes represent genetic changes that reduce the likelihood of successful gene flow. In this graph, blue individuals can mate with green or red individuals, but red and green individuals are reproductively incompatible. Allopatric speciation involves these three steps: (1) Populations encounter a barrier, (2) reproductive isolation (RI) completes in allopatry, and (3) isolates persist. Note that the barrier's effectiveness changes over time. According to Jansson & Dynesius (2002), if this barrier does not persist for at least 100 thousand years, reproductive isolation for taxa with long generation times will not likely be complete. The right-hand column lists the different hypotheses that correspond to the stage of speciation (see Table 1). (b) This schematic shows the factors that influence the probability of parapatric or sympatric speciation as in panel a. The green shading represents a novel habitat or trophic resource. Note that the olive green phenotype has greater fitness in the green shaded habitat/resource, and the dark green phenotype evolves from olive green progenitors and is even more specialized to the novel habitat/resource. Dark-green X blue crosses produce hybrids that do not have high fitness in either habitat/resource.

from too much inbreeding or have lower phenotypic variability; thus, they may be less able to adapt to changing environments (Kisel et al. 2011).

Although initial tests of the area hypothesis found no support for a clear relationship between biome or bioregion area and species richness (Willig et al. 2003), Fine & Ree (2006) pointed out that area and time are inextricably linked. Because speciation and extinction are processes that take time (often up to millions of years), a fair test of the effect of area must include a temporal component. Two related hypotheses, the time-integrated area hypothesis (Fine & Ree 2006) and the tropical conservatism hypothesis (Wiens & Donoghue 2004), consider both time and area and make the same prediction: Because tropical biomes are larger (over some interval of time), they should have higher diversification rates (over large amounts of time) than temperate

biomes. Temperate regions are just as old as tropical regions. The important difference between them is that temperate regions have covered smaller areas over the past 100 million years or so, owing to major changes in global climate, which has been reducing the relative areas of tropical environments and increasing the extent of temperate environments since the Oligocene. A second important difference is the frequent glaciation that has caused temperate areas to fluctuate in extent and location over the past two million years (Willis & McElwain 2002, Mannion et al. 2014). Nevertheless, temperate bioregions have continuously existed in some extent from at least 50 million years ago up to the present in North America, South America, Eurasia, Africa, and Australia (Willis & McElwain 2002). These temperate bioregions have also harbored mammals, birds, reptiles, amphibians, and seed plants throughout this time period (Willis & McElwain 2002, Jiménez-Hidalgo et al. 2015, Kerkhoff et al. 2014).

Population sizes should also correlate positively with available energy (e.g., productivity) (Wright 1983, Allen et al. 2007). Thus the mechanisms described above for how geographic range size and genetic diversity relate should be on average greater in larger bioregions, increase the probability of speciation and reduce the probability of extinction, and be even more accentuated in high productivity versus low productivity bioregions (Jetz & Fine, 2012, Hurlbert & Stegen 2014). This is similar to the concept of community abundances from the metabolic theory of ecology, which hypothesizes that more available energy within a region allows species to have larger average population sizes, influencing their speciation and extinction probabilities (Allen et al. 2007). In addition, high productivity bioregions should have greater overall environmental heterogeneity (including availability of trophic resources) than low productivity bioregions, increasing the potential for parapatric speciation within bioregions (Kisel et al. 2011).

Note that the role of energy considered here so far is how it influences the probability of speciation and extinction within regions. This is separate from the hypothesis that total energy availability limits the total number of species within a region, which I briefly discuss next.

3.2. Area, Energy, and Ecological Limits

A different perspective on the drivers of coexistence at the regional scale is the hypothesis that there is a carrying capacity for species within regions, which is determined by the amount of available resources, such that regions achieve an equilibrium of species diversity balanced by immigration or speciation and extinction. In its simplest form, this theory is agnostic to the niche differences of species. It reasons that any addition of a new species to an area causes a reduction in the average population size of all resident species, thus increasing extinction rates, because there can be a limit on the number of individuals (of any species) in an area. Thus, each arrival is balanced by the extinction of a resident species (Rabosky & Hurlbert 2015).

Because species do have ecological differences, a related argument has been made that closely related species compete strongly with one another, as they are likely to be ecologically similar; thus, over time, diversification rates of clades slow down, resulting in a pattern of diversity-dependent diversification (reviewed in Foote 2010). The assumption is that each species is competing with close relatives for some share of the resource pool in a zero-sum game, and there is an ecological limit dictated by energy availability that determines the total possible number of species for each clade within regions. Dozens of phylogenetic studies have reported diversity-dependent diversification (reviewed in Rabosky 2013), although there are many methodological problems and sampling issues with attributing these slowdowns to diversity dependence (Wiens 2011, Rabosky & Hurlbert 2015). Harmon & Harrison (2015) concluded that the pattern of diversity-dependent slowdowns is most likely a statistical artifact rather than an indication that clades experience limits to diversification.

This is not to say that ecological traits of co-occurring species do not affect their diversification rates. Abundant examples of how species interactions can influence speciation and extinction have been found (reviewed in Kisel et al. 2011, Cornell 2013, Rabosky 2013). Nevertheless, it is extremely difficult to disentangle the effects that area and resources may have on the intrinsic clade-level traits that promote speciation and persistence in lineages from how area and productivity may impose some sort of limit on diversity (Kisel et al. 2011). Moreover, the ecological limits theory has not identified a clear logical link between how the amount of resources is connected to a carrying capacity for the total number of individuals across all species and thus how resources can be directly linked to species diversity (Brown 2014). Previous reviews showing little support for the species-energy hypothesis noted that large-scale patterns of species diversity did not correlate strongly with numbers of individuals (Evans et al. 2005, Brown 2014). Although new immigrants to a region (or new species evolving in situ) undoubtedly use some share of the available resources of a region, how a new species would reduce the community abundances of *all* other resident species is unclear, unless only one other species occurs in the region. Given some amount of resources and some standing species diversity, the relative abundances of each of these species can vary in infinite ways (Hubbell 2001). In addition, empirical studies have shown that common species can have extremely large relative abundances in a region (ter Steege et al. 2013). If newcomer species reduce the abundances of common species but not of the rarer species, then more rare species could be easily accommodated within the region.

Our understanding of how relative abundances of each resident species may shift over time is complicated by the fact that the sizes and shapes of bioregions expand and contract in 14-, 21-, and 100-thousand-year Milankovitch cycles, which are shorter than most waiting times for speciation and extinction (Rosenblum et al. 2012). Moreover, many bioregions like tundra and boreal bioregions are unlikely to be at equilibrium diversity for trees or vertebrates given their young histories (Fine & Ree 2006). Finally, which empirical data needs to be collected to test whether bioregions are at a carrying capacity for species diversity is unclear. Instead, I believe it is more productive to focus on how various drivers may affect speciation and extinction, without worrying about whether or not a bioregion represents an equilibrium or nonequilibrium system (**Figure 1**).

3.3. Evaluating Time-Integrated Area and Energy and Tropical Conservatism

Because species-energy, the time-integrated area, and the tropical conservatism hypotheses rely on the same mechanistic bases relating population size to speciation and extinction rates, I combine them here. The prediction of these hypotheses is that integrated measures of area and energy over time should correlate with species diversity or diversification rates of bioregions at large taxonomic and temporal scales.

Two studies have correlated extant species diversity with bioregional area over time. Fine & Ree (2006) calculated time-integrated area of 11 boreal, temperate, and tropical bioregions since the Miocene, Oligocene, and Eocene, and each significantly correlated with extant tree diversity, with older time-integrated area measures yielding the strongest R^2 values. Jetz & Fine (2012) correlated time-integrated area (together with available energy) with regional and endemic diversity of four vertebrate groups (birds, mammals, reptiles, and amphibians) and found significant correlations, although models that also included temperature yielded the lowest likelihoods.

Fossil studies of both marine and terrestrial clades have generally found higher speciation (origination) rates in tropical regions (reviewed in Mittelbach et al. 2007). Jablonski et al. (2006, 2013) found that lineages of marine bivalves originated in the tropics and often spread into the temperate zone while maintaining their tropical presence (the out-of-the-tropics pattern). Because

of these spillover species, the latitudinal gradient is more muted (but still present). This tendency of marine species to span biomes may be due to the shallower temperature gradient in marine compared with terrestrial ecosystems and the greater potential for long-distance passive dispersal in marine ecosystems. The patterns exhibited by marine bivalves are fundamentally similar to terrestrial organisms, however, in the sense that transitions across biomes are heavily asymmetric with very few colonizations of the tropics from temperate clades (Jablonski et al. 2013).

Phylogenetic studies of large clades can also provide insight into the importance of area/energy/time in generating diversity gradients. Although these studies are rarely conducted at the bioregional scale, most of them include temperate versus tropical comparisons. For example, Kerkhoff et al. (2014) compared the phylogenetic diversity of over 12,500 species of New World woody angiosperms from temperate and tropical biomes with the timing of interbiome transitions. They found results consistent with the tropical conservatism hypothesis: Colonization of the temperate zone by a smaller subset of tropical lineages coincided with global cooling events, and tropical regions accumulated more species over time. Similar patterns have been reported in mammals (Buckley et al. 2010), butterflies (Hawkins 2010, Condamine et al. 2012), and amphibians (Wiens et al. 2010, Kozak & Wiens 2012).

Pyron & Wiens (2013) integrated a phylogeny of 2,871 amphibian species with distribution records of 6,117 species (out of ca. 7,000 total amphibian species in the world) and applied the GeoSSE algorithm, which attempts to disentangle speciation, extinction, and dispersal rates among regions. They estimated higher speciation rates and lower extinction rates in the tropics and higher extinction rates in the temperate zone for amphibians. Pyron (2014) conducted a similar analysis by integrating a phylogeny of 4,161 squamate reptiles with distribution records of all 9,416 species worldwide and found the same pattern: higher extinction in the temperate zone, and higher speciation and lower extinction rates in the tropics. Rolland et al. (2014) investigated the phylogeny and biogeography of 5,020 mammal species (92% of the world's total) and, using the same GeoSSE algorithm, found higher speciation rates and lower extinction rates in tropical regions and higher extinction rates in the temperate zone. Several studies of birds have reported higher diversification rates of birds in tropical regions compared with temperate regions (Cardillo et al. 2005, Ricklefs 2006). In a comprehensive sample of 9,993 bird species, however, Jetz et al. (2012) found no significant trend in diversification rate shifts among nodes with latitude, but overall, tropical regions accumulated more species (both from clades with high and those with low diversification rates).

Methodological concerns about the accuracy of estimating extinction rates with the GeoSSE algorithm have been raised because this model does not permit heterogeneity in diversification rates and thus may be subject to high type 1 error (Rabosky & Goldberg 2015). For example, a reanalysis of Rolland et al.'s (2014) data set using different methods that included rate heterogeneity found no strong latitudinal difference in diversification rates (Belmaker & Jetz 2015); this result was similar to that found in birds (Jetz et al. 2012). This same study, which is the first to investigate phylogenetic data across the 32 bioregions defined by Jetz & Fine (2012), found strong support for time-integrated area in explaining global diversity patterns in birds and mammals (Belmaker & Jetz 2015). Their statistical model included diversification rates, time-integrated area, temperature, and productivity and found that time-integrated area by far explained the most variance compared with the other included variables.

In summary, although it is difficult to disentangle the signals of speciation and extinction in phylogenetic studies of diversification, all of the large-scale phylogenetic analyses recover results consistent with the tropical conservatism hypothesis and the area/energy/time hypothesis, namely that tropical bioregions have been accumulating species to a greater degree than extratropical bioregions.

3.4. Climate Stability

Bioregions closer to the equator experience greater climate stability than bioregions closer to the poles, meaning that low elevation equatorial bioregions have smaller temperature fluctuations during the year (Janzen 1967). The climate stability of low latitudes extends to longer timescales—decades, millennia, and even longer due to Milankovitch cycles caused by periodic changes in the Earth's orbit, tilt, and spin—as well as global cooling events driven by changing continental configurations affecting ocean currents and atmospheric CO₂ levels (Willis & McElwain 2002). Within a single year, temperate regions experience summer and winter; thus, temperate organisms have to withstand large temperature changes compared with tropical organisms. This observation led Janzen (1967) to postulate that mountains should be more effective as a barrier for dispersal and gene flow in the tropics because tropical organisms should be adapted to a smaller range of temperature variation during the year than temperate organisms.

Extending these ideas to larger timescales, Dynesius & Jansson (2000) and Jansson & Dynesius (2002) reasoned that climatic stability should also be greater toward the equator over millennial to million-year scales, because Milankovitch cycles of 12, 41, and 100 thousand years always cause greater climate change in extratropical areas than in tropical areas. Because speciation events in many clades generally require more than 100 thousand years (Stanley 1985, Sepkoski 1998, Rosenblum et al. 2012), organisms experiencing climatic instability [or in the words of Dynesius & Jansson (2000), greater Orbital-forced Range Dynamics] also experience strong selection pressures to increase their dispersal ability and to widen their environmental tolerances, resulting in increases in geographic range size (Stevens 1989). Indeed, studies on both invertebrates and vertebrates have found wider thermal tolerances in temperate compared with tropical organisms (Ghalambor et al. 2006, Deutsch et al. 2008). Moreover, if organisms inhabiting regions with greater climatic stability encounter habitat or resource heterogeneity, they are more likely to become specialized to either a particular habitat or a trophic resource, because there is sufficient time (i.e., more than 100 thousand years) for divergent selection and speciation to operate (Futuyma & Moreno 1988, Sheldon 1996, Dynesius & Jansson 2000, Jansson & Dynesius 2002). Thus, the incidence of habitat (and trophic) specialization should be more common in climatically stable tropical bioregions, leading to greater frequency of parapatric and sympatric speciation (Moritz et al. 2000). Greater habitat specialization in stable bioregions should therefore be reflected in increased β -diversity (as measured by environmental heterogeneity, not geographic distance, per se) in low-latitude bioregions.

Habitat specialization and trophic specialization can be considered the inevitable consequences when organisms encounter a divergent resource gradient in which adaptations that confer success associated with one habitat or resource come at a cost in fitness in the second habitat or resource. For example, beak size in large-beaked and small-beaked Darwin's finches confers an advantage for only one food resource, with intermediate sizes suboptimal for both taxa (Grant et al. 2004). Similarly, serpentine tolerance in plants requires energy investment in enzymes to deal with an excess of magnesium—energy that could otherwise be invested in growth. This investment prevents serpentine-tolerant plants from keeping pace with competitors in nonserpentine soils (Kay et al. 2011). These kinds of resource gradients that promote evolutionary trade-offs occur throughout the globe. The important consideration is not only how much time is required for specialization to occur, resulting in speciation, but also how likely is it that incipient specialists persist? If the formation of complete, reproductively isolated species takes more than 100 thousand years, successful lineage divergence resulting in a net gain of species within a region is more likely in stable climates (Jansson & Dynesius 2002). In unstable climates, new isolates specialized to resources or habitats often do not persist when climates change, due to either local extinction or incomplete

reproductive isolation and thus gene flow with neighboring isolates (the concept of ephemeral divergence of Futuyma 2010). For example, three-spine sticklebacks, although capable of rapidly speciating in high latitude lakes, also experience high extinction rates and do not exemplify a particularly diverse lineage (Rabosky 2013). Similarly, large-beaked and small-beaked species of Darwin's finches during El Niño events on the Galápagos Islands have experienced elevated hybridization when resource supplies changed, suggesting that the two species could undergo fusion with continued unstable climates (Grant et al. 2004).

Climate stability is also hypothesized to directly impact probabilities of extinction. Although organisms with high dispersal capabilities are able to track climate change and thus escape extinction, those with lower dispersal abilities (and/or those confined to smaller bioregions) are expected to experience greater extinction rates in high latitude regions (Dynesius & Jansson 2000, Graham et al. 2006, Sandel et al. 2011). More stable bioregions, in contrast, act as refugia and promote low extinction rates (Carnaval et al. 2009, Sandel et al. 2011, Fjeldså et al. 2012).

The climate stability hypothesis is complementary to the area/energy/time hypothesis in the sense that it has a similar mechanistic basis: the effect of geographic range size and genetic diversity of populations and, in turn, how these factors influence speciation and extinction rates. Building on predictions of how larger geographic ranges and greater genetic diversity should influence speciation and extinction rates, the climate stability hypothesis posits that these factors should be strongly mediated by orbitally forced range dynamics. Thus, the time-integrated area of high latitude bioregions is likely to fluctuate greatly during cold periods and cause high extinction rates. Because these temperature minima can greatly increase extinction rates, measuring the cumulative time-integrated area may not be the best way to test the relationship between overall area available for populations within regions and species richness. Instead, if bioregion contraction has caused massive extinctions, calculation of the time-integrated area using the lowest minimum area should be more accurate. For example, Fine et al. (2008) correlated the minimum size of 11 boreal, temperate, and tropical bioregions during the Pleistocene with extant tree diversity and found a significant and positive relationship. The recent global phylogenetic studies of mammals, amphibians, and squamate reptiles mentioned in Section 3.3 (Pyron & Wiens 2013, Pyron 2014, Rolland et al. 2014) all found strong signatures of extinction rates at high latitudes, which is consistent with the climate stability hypothesis (Hurlbert & Stegen 2014; but see Rabosky & Goldberg 2015). Smaller scale phylogeographic studies that have compared paleoclimate models with genetic diversity of organisms associated with latitudinal gradients in climate stability have found strong signals that climate stability reduces local extinction and promotes population genetic diversity (Carnaval et al. 2009, Fjeldså et al. 2012), with effects especially pronounced in organisms with low dispersal capabilities (Graham et al. 2006).

Only a few studies have attempted to correlate species richness with direct measures of climate stability. Two global studies have found a strong negative correlation between absolute climate change since the Last Glacial Maximum (Jansson 2003) and climate velocity (an integrated measure of climate change over time and space) (Sandel et al. 2011) during this time for both plant and vertebrate endemism, especially for vertebrates with low dispersal ability. Jansson & Davies (2008) compared 86 sister pairs of angiosperm families and found significant negative correlations between species diversity and mean Pleistocene temperature variation.

In marine systems, Valentine & Jablonski (2015) evaluated global patterns of extant marine invertebrate diversity in shallow seas and deep sea benthic zones. They reported that in shallow seas bivalve diversity correlates positively with temperature, yet in deep seas, which are always approximately 4°C, marine invertebrates can be even more diverse than in shallow seas. Neither shallow nor deep sea invertebrate diversity correlates with productivity at large scales. The one common factor shared between regions containing highly diverse marine invertebrate faunas is

Table 2 These examples illustrate how species diversity, temperature, productivity, and climate stability are related to each other in terrestrial and marine systems. As shown in bold, only climate stability consistently correlates with species diversity in these examples from marine and terrestrial systems

System	Species diversity	Temperature	Productivity	Climate stability	Selected references
Trees and vertebrates in boreal forests	Low	Low	Low	Low	Fine et al. 2008, Jansson & Davies 2008, Jetz & Fine 2012
Trees and vertebrates in tropical forests	High	High	High	High	Fine et al. 2008, Jansson & Davies 2008, Jetz & Fine 2012
Marine invertebrates in tropical shallow seas	High	High	Moderate to low	High	Tittensor et al. 2010, Valentine & Jablonski 2015
Marine invertebrates in temperate shallow seas	Low	Low	High	Low	Belanger et al. 2012, Valentine & Jablonski 2015
Marine invertebrates in deep benthic seas	High	Low	Extremely low	High	Rex & Etter 2010, Valentine & Jablonski 2015

stability in climate and resource supply (**Table 2**). High temperature, shallow seas have stable water columns and a steady (but moderate) supply of productivity. Deep water seas are not productive at all, but resource availability does not vary appreciably in time (Rex & Etter 2010).

Global β -diversity studies generally find positive correlations between species turnover and latitude (Qian & Ricklefs 2007). At very small scales, this pattern has been demonstrated to be driven by regional pool differences (Kraft et al. 2011, Lessard et al. 2012). However, the β -diversity pattern that is predicted by the climate stability hypothesis represents large-scale, between-habitat turnover, not small-scale turnover within a relatively homogenous environment (i.e., Kraft et al. 2011). Studies that have specifically investigated between-habitat turnover (for example elevational gradients) have found greater specialization at low latitudes (Rahbek & Graves 2001, Ghalambor et al. 2006, Kozak & Wiens 2012). Similarly, specialization to serpentine soils is much more prevalent in tropical areas compared with temperate areas, consistent with predictions of the climate stability hypothesis (Jansson & Dynesius 2002, Anacker 2011). Criticisms of the climate stability hypothesis have suggested that recent glaciation events cannot serve as a general explanation for the latitudinal diversity gradient (Mittelbach et al. 2007), because strong latitudinal diversity gradients have been reported from paleontological studies much farther back in time (e.g., Crame 2001). However, a recent evaluation of the latitudinal diversity gradient from the past 500 million years suggests that a steep biodiversity gradient from the poles to the equator occurs only during ice house climates like the past 30 million years (Mannion et al. 2014). During greenhouse climates, the gradient becomes shallower or reverses, such that the world has had biodiversity peaks in temperate latitudes (Mannion et al. 2014). A so-called greenhouse world represents a world with much greater climate stability worldwide, whereas an ice house world experiences much greater climate fluctuations, with extinctions at the poles and a steep diversity gradient (Archibald et al. 2010; but see Powell 2007). Notably, this is the very pattern that the climate stability hypothesis would predict.

3.5. Temperature and Evolutionary Speed

Rohde (1992) proposed that because temperature has a direct and positive affect on the speed of physiological processes in ectotherms, effective evolutionary speed should be higher in warmer

areas. Unlike the previous set of hypotheses, the evolutionary speed hypothesis focuses only on mutation rates, generation time, and the overall effective speed of selection (adaptation) and how these increases may influence speciation rates. In theory, evolutionary speed could ramp up speciation rates in two different ways. First, the simple increase of mutation rates, all else being equal, could increase the chances that divergent populations evolve reproductive isolation. Second, and more complicated, faster metabolic rates should lead to shorter generation times, which, combined with faster mutation rates, should also increase the rate at which natural selection occurs. This phenomenon may lead to faster evolution to novel environments, followed by increased rates of specialization, divergent selection, and speciation (Allen et al. 2007).

The evolutionary speed hypothesis also predicts that speciation should be higher in warmer bioregions due to the effect that temperature has on promoting reproductive isolation. This prediction has been tested by several indirect methods: correlating species richness with temperature, comparing rates of molecular evolution of sister clades, and comparing the diversification rates of temperate and tropical clades. Some studies have shown strong correlations of temperature with the species richness of terrestrial and marine invertebrates (Gillooly et al. 2005, Allen et al. 2006, Tittensor et al. 2010; but see Hawkins et al. 2007). However, the cold (4°C), climatically stable deep sea invertebrate communities of the North Atlantic discussed above have exhibited extraordinarily high species richness—much higher than neighboring warmer and more productive (but climatically unstable) shallow sea environments (Rex & Etter 2010, Valentine & Jablonski 2015). These data cast doubt on the overall generality of the relationship between temperature and speciation, although marine invertebrates may somehow be outliers.

Sister species comparisons have found some instances of higher molecular evolution in tropical versus temperate plants (Davies et al. 2004, Gillman et al. 2010). Gillman et al. (2009) compared sister groups from 260 mammal species from 10 orders and 29 families and found higher substitution rates in the Cytochrome b gene for warmer versus cooler sister species. Recent large-scale phylogenetic studies that have reported higher rates of diversification in tropical clades (Pyron & Wiens 2013, Pyron 2014, Rolland et al. 2014) are broadly consistent with all hypotheses that predict higher diversification rates in the tropics (**Table 1**). However, two recent studies using the comprehensive phylogeny of birds found no differences in diversification rates, and these data were presented as evidence to reject the evolutionary speed hypothesis (Jetz et al. 2012, Rabosky et al. 2015). Nevertheless, bird and mammal groups, being endotherms that regulate their metabolic rates, are not the ideal study systems to test the evolutionary speed hypothesis.

More importantly, the evolutionary speed hypothesis does not enjoy general support because reproductive isolation (and natural selection in general) does not appear to be limited by mutation rates (Coyne & Orr 2004, Mittelbach et al. 2007). Although faster effective evolutionary speed should promote adaptation to novel environments and thus influence parapatric speciation rates, attribution of this process to temperature, per se, rather than to other drivers such as productivity, climate stability, or biotic interactions is difficult (see Section 3.6). The finding that organisms living in warmer climates have greater rates of molecular evolution would also be predicted by many of the hypotheses in **Table 1**. For example, bioregions with large area/energy/time should have higher average population sizes (**Figure 1**), and larger populations are predicted to have greater genetic diversity than smaller populations (Kisel et al. 2011). In fact, although Davies et al. (2004) reported higher rates of molecular evolution in 86 tropical/temperate sister pairs of angiosperm families, they rejected the evolutionary speed hypothesis, because the effect of temperature on species richness was found to be direct and not driven by molecular rates of evolution. One potential way forward may be the direct effect that temperature has on seasonality (Pianka 1966, Archibald et al. 2010). Bioregions with less seasonality may select for shorter generation times in some groups of organisms, causing faster molecular evolution and higher rates of speciation.

A recent study on Amazonian trees found that diversification rate of tree clades correlated with turnover time in long-term plots and that the tree clades with fast turnover (which is associated with shorter generation time) were also the most diverse and accounted for a majority of all stems (Baker et al. 2014). Another possibility is that temperature increases the possibility of biotic interactions to promote coevolutionary arms races (Brown 2014; and see Section 3.6).

In summary, general support for the evolutionary speed hypothesis is lacking. However, phylogenetic data sets of endotherms represent especially weak tests of this hypothesis given that the hypothesis makes specific predictions about the speciation process only in ectotherms and makes no predictions whatsoever about extinction probabilities. Thus, future tests of this hypothesis should instead focus on experimental studies of speciation in ectotherms and plants (see discussion on p. 325, Mittelbach et al. 2007) that measure not only selection-driven change but also control for generation time and population size. Studies of this sort could be augmented by empirical studies of the phylogeography and population genetics of species (and close relatives) of ectotherms and plants at different latitudes to disentangle the importance of temperature from generation time and population size.

3.6. Biotic Interactions

All bioregions contain species from multiple trophic levels, yet the organisms within some bioregions may interact more intensely with one another, which could influence speciation and extinction for several different reasons. In a recent review of latitudinal patterns of predation, herbivory, and mutualisms, Schemske et al. (2009) presented evidence that tropical regions had stronger biotic interactions than temperate regions. Although very few comparative studies had used the same methods to rigorously measure the strength of interactions across latitudes (e.g., Freestone et al. 2013), they found that the evidence gleaned from multiple sources overwhelmingly suggests that biotic interactions are more intense in tropical systems than temperate systems. There are four hypotheses by which stronger biotic interactions could influence diversity—two that involve speciation (enemy-mediated habitat specialization and the geographic mosaic of coevolution) and two that relate to the persistence and maintenance of species diversity (competition causing finer niches and predation promoting coexistence).

First, biotic interactions could contribute to greater habitat specialization by plants in climatically stable bioregions. When neighboring habitats differ strongly in resource availability (e.g., white-sand forests next to clay-soil forests or seasonally dry habitats next to a riparian area), plants incur more energetic costs to replace tissues they lose from herbivores or pathogens in low-resource than in high-resource habitats (Janzen 1974). This should drive selection for investment in plant defenses and, because of allocation trade-offs, higher investment in plant defense should lead to slower growth rates, reducing competitive ability in high-resource habits (Coley et al. 1985, Fine et al. 2004). This enemy-mediated habitat specialization effect has been hypothesized to be more pronounced in tropical than extratropical bioregions (Fine et al. 2013) because there are more enemies in productive, stable climates and thus stronger enemy pressure (Salazar & Marquis 2012, Lim et al. 2015). As already noted in Section 3.4, some evidence that habitat specialization is more prevalent in tropical bioregions has also been found. Several Amazonian studies have found evidence that herbivores enforce habitat specialization through selection for a trade-off between growth and defense (Fine et al. 2004, 2013). However, there has been no systematic comparison of this phenomenon in bioregions at different latitudes.

Second, Schemske (2009) posited that divergent selection and speciation probabilities among interacting partners of antagonistic or mutualistic species should be higher in tropical regions. He reasoned that in the tropics, organisms are not generally killed by abiotic stresses, and thus

a greater proportion of the selective regime in the tropics should be driven by biotic agents. These agents can themselves evolve in response, spurring evolution in both partners (Schemske 2009). Moreover, tropical environments with low seasonality (moist and rain forests) support more abundant interacting partners (plants, herbivores, pathogens, predators, mutualists, etc.), and these antagonistic and mutualistic interactions can occur during a great majority (or throughout) the entire year. In colder or drier bioregions, by comparison, seasonal dormancy interrupts these interactions, delaying the speed of coevolution. Thus, effective evolutionary speed of coevolution should be faster in productive, stable climates like tropical bioregions. Ehrlich & Raven's (1964) escape and radiate hypothesis predicted that plants with novel defenses become immune to enemies and greatly expand their ranges, promoting allopatric speciation rates, whereas counter-adaptation by specialist enemies subsequently causes range contraction. Similarly, specialization can lead to speciation by driving host race formation or by increasing the patchiness of specialist geographic ranges, leading to differentiation (Thompson 1994, Janz et al. 2006). These mechanisms also have the potential to become stronger over time, generating a positive feedback loop (Schemske 2002).

As noted by Schemske (2009), no studies have evaluated the role that biotic interactions may have on speciation rates across latitudes, and in general, very few studies have investigated how coevolutionary arms races may influence diversification in enemies or their host plants (Futuyma & Agrawal 2009). Nevertheless, results of some studies are consistent with more intense interactions between plants and their enemies in tropical regions (Coley & Barone 1996, Lim et al. 2015). For example, African tropical lowland forest bird communities harbor more specialist parasites and greater parasite diversity than highland and fynbos bird communities (Loiseau et al. 2012).

Moreover, investment in antiherbivore defense by plants is greater in tropical regions (Coley & Barone 1996), and closely related tropical plant species often have extremely divergent chemical defense profiles (Becerra 1997, Kursar et al. 2009, Fine et al. 2013). Farrell et al. (1991) showed that the evolution of resins or latexes in plant lineages, many of which are tropical, led to significant increases in host plant diversity. From the enemies' side, adaptation to a new host can result in significant diversification increases (Janz et al. 2006). On the other hand, the timing of many plant radiations has been shown to predate the arrival of their insect host-specialists, suggesting that plants and insects often may radiate independently and not as a product of their interaction (Winkler & Mitter 2008, Forister et al. 2012).

3.7. Biotic Interactions and Finer Niches

Two longstanding hypotheses posit that organisms in regions with stronger biotic interactions have finer niches—in terms of either their resource usage or habitat, or their interactions with natural enemies. First, stronger competition could drive niche divergence, resulting in finer niches per species; thus, more species could coexist in a community (Dobzhansky 1950, Pianka 1966). This hypothesis that competition causes finer niches has not been well supported by empirical evidence. Vasquez & Stevens (2004) studied 13 clades of birds, mammals, insects, and plants and found no evidence of finer niche subdivision in tropical forests compared with temperate forests. Hyperdiverse groups like trees and birds in tropical rainforests are characterized more by functional redundancy than niche specialization. For example, more than 80% of the thousands of species of neotropical trees are shade tolerant, and despite attempts to characterize microhabitat and gap-size disturbance requirements, shade-tolerant species do not appear to finely partition abiotic gradients (Hubbell 2005). Ricklefs (2010) investigated correlations between niche overlap and species richness in taxonomic groups of birds and also found an overwhelming pattern of functional redundancy.

Second, stronger predation (or herbivory) could drive selection for divergent antipredator defenses in prey (or plants). If these defenses underlie predator–prey specialization, prey (or plants) would compete for enemy free space, allowing greater prey (or plant) coexistence. Under the Janzen–Connell hypothesis (Janzen 1970, Connell 1971), host-specialist enemies (insect herbivores, seed predators, or fungal pathogens) readily locate newly dispersed seedlings by already living in the canopy of a mother tree or by using cues to locate fruiting host trees. These enemies cause massive mortality of seedlings dispersed beneath the canopy, and only seeds dispersed farther away from the mother tree escape predation (Janzen 1970, Connell 1971). Rare species gain an advantage (the rare species advantage) because their seedlings are almost never dispersed under the crowns of a different conspecific tree. At the community level, the rare species advantage serves to prevent competitive exclusion of any tree species.

In the past 40 years, the Janzen–Connell hypothesis has enjoyed much empirical support (Terborgh 2012). However, very few studies have compared density-dependence in trees across different bioregions (Hille Ris Lambers et al. 2002, Johnson et al. 2012). Johnson et al. (2012) found a latitudinal gradient in density dependence, although they did not include any tropical sites. Hille Ris Lambers et al. (2002) found that the prevalence of density-dependence was similar in temperate and tropical forests. However, the authors did not quantify the strength of density-dependence; thus, this study cannot refute the hypothesis that Janzen–Connell effects causing a rare species advantage may be promoting coexistence in tropical bioregions compared with temperate bioregions. Although I know of no study that has compared host-specific pathogen attack across temperate and tropical forests, fungal pathogens have been implicated in driving tree relative abundance patterns (Mangan et al. 2010), and one small study in the Amazon basin found correlations between plant diversity and fungal pathogen operational taxonomic unit diversity at both α and β scales (Peay et al. 2013). This finding is consistent with the Janzen–Connell hypothesis.

In summary, biotic interactions have been hypothesized to increase speciation rates through increased habitat specialization and coevolutionary arms races and to reduce extinction rates by promoting coexistence. Because biotic interactions have not been studied within a consistent comparative framework across bioregions, an evaluation of their importance at the present time is difficult. Many studies are suggestive, but few are conclusive (Schemske et al. 2009).

4. CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Large-scale phylogenetic studies of trees, birds, mammals, squamate reptiles, and amphibians all show that tropical bioregions are the source for a great majority of clades and are composed of a mixture of ancient and recently derived lineages and that temperate bioregions harbor a subset of these lineages. These results are consistent with the hypothesis that the large extent of tropical environments during the past 10–50 million years, combined with the greater climatic stability of the tropics, has promoted speciation and reduced extinction in tropical bioregions and that niche conservatism has kept most tropical lineages from spreading into temperate climates. Energy availability appears to contribute only in an indirect way to mechanisms underlying global patterns, especially considering that marine diversity gradients can sometimes be completely decoupled from temperature and productivity gradients. Instead, climate stability (and thus stability of resource supply) and the time–integrated area of bioregions together represent the most important drivers of both terrestrial and marine global species richness patterns. Productivity and temperature directly impact seasonality, available resources for trophic interactions, and the average population sizes of taxa within bioregions. Biotic interactions likely augment both diversification and coexistence in tropical bioregions.

Delimiting the appropriate temporal, taxonomic, and spatial scales by which to test the time-integrated area and climate stability hypotheses remains a challenge. Critics of the time-integrated area and tropical conservatism hypotheses have voiced concerns about how to choose the appropriate window of time to evaluate time-integrated area (Mittelbach et al. 2007). For example, studies report that vertebrate species have average lifetimes of approximately 10 million years (Stanley 1985, Rosenblum et al. 2012). If generally true, what does the time-integrated area of a bioregion during the past 55 million years have to do with its extant diversity? This is a valid criticism, but at its core one that can be tackled with empirical data. Now that fossil-calibrated, comprehensive phylogenies of extant species are becoming available for more and more of the tree of life, an investigator may answer questions like, "What is the age distribution of all of the mammal species in a bioregion?" By mapping geography onto a phylogeny of all mammals, one can determine how long lineages have been in any particular bioregion and calculate the window of time that would account for a crown group that would include the evolutionary history of, for instance, 70%, 80%, or 90% of the extant species within a bioregion. The time-integrated area of a bioregion could then be estimated using paleoclimatic reconstructions of that bioregion (see Fine & Ree 2006) from the temporal cutoff that was indicated by the phylogeny. Providing precise measures of climate stability during that time is difficult; however Jansson (2003), using global circulation models, showed that climate stability since the Last Glacial Maximum can serve as a proxy for climate stability across much deeper time periods and that new global climate layers now extending back 120,000 years make it possible to determine stability through a full glacial and interglacial period (Fuchs et al. 2013, Tolley et al. 2014). Finally, recent algorithmic developments have improved static estimates of climatic stability into a more dynamic model that can incorporate both sea level rise and contraction as well as the dispersal ability of organisms (Graham et al. 2010). These developments enable much more accurate modeling of habitat area through time.

I envision this kind of analysis being conducted for all of the major clades of the tree of life. I emphasize that this approach is best applied to large, inclusive clades of organisms (e.g., birds) rather than narrowly defined clades (e.g., penguins) because each individual clade has intrinsic traits that mediate speciation and extinction probabilities in idiosyncratic ways across their evolutionary and biogeographic history (Coyne & Orr 2004). For each clade, the number of bioregions that best described the evolutionary arenas for that clade may be somewhat different, and the time-integrated area and climate stability measures may also correspond to different windows of time. Each of these bioregions would also be measured for available energy, temperature, topographic and edaphic heterogeneity, species richness, and β -diversity. These large-scale bioregional tabulations could be coupled with experimental and fine-scale studies of biotic interactions across all bioregions. For example, studying clades of plants and their associated natural enemies in multiple bioregions should yield data on the relative strength of biotic interactions on coevolution and habitat specialization. Finer-scale observational and experimental studies in geographically distant, replicated sites within multiple bioregions can explore the degree to which chemical defense innovation matches up with host-specialist enemy counteradaptation and whether these processes result in greater phenotypic and molecular divergence in tropical compared with temperate bioregions.

By analyzing multiple clades together in this way, this research would generate a large number of independent, replicate bioregions (both marine and terrestrial) that could be used to test the various drivers of species richness. Although terrestrial vertebrate biologists can boast of global distribution maps and comprehensive phylogenies, invertebrates, plants, and fungi are still severely undersampled, and most of these unknown taxa inhabit tropical forests (Tedersoo et al. 2014). For example, at least 6,000 of the 16,000 estimated tree species in the Amazon have not yet been described (ter Steege et al. 2013). In my opinion, it is impossible to understand the processes which generate biodiversity without first having a more complete description of the tree of life.

This investment in taxonomy and natural history should be our top priority, especially in this time of massive, accelerating, and destructive anthropogenic change.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I thank Gary Mittelbach, Margaret Metz, Dan Rabosky, Jim Valentine, Rauri Bowie, Walter Jetz, David Armitage, and my Fall 2014 Integrative Biology 250 graduate seminar class for valuable discussions. Support was provided by National Science Foundation grant DEB 1254214.

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