What explains patterns of biodiversity across the Tree of Life?

New research is revealing the causes of the dramatic variation in species numbers across branches of the Tree of Life

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A major challenge in biology is to explain why some groups have thousands or millions of species whereas others have few. Here, I review the causes of this variation. New studies reveal that higher species numbers in many major groups are explained by higher diversification rates (and traits that accelerate these rates). These traits span most of biology (e.g. genomics, ecology, morphology). Rather than simply testing individual traits, research should now focus on comparing how much variation in diversification rates is explained by different types of traits. For example, is local-scale ecology (e.g. microhabitat, diet) more important than large-scale climate (e.g. occurring in tropical vs. temperate regions)? Are traits based on particular values (e.g. smaller body sizes) more important than those based on rates of change (e.g. faster size evolution)? I review recent results on the relative importance of different traits for driving diversification, and present a framework for future research.

Keywords:
biodiversity; diversification; extinction; niche; speciation; species richness

Additional supporting information may be found in the online version of this article at the publisher's web-site.

DOI 10.1002/bies.201600128

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Introduction

A major challenge in biology is to explain differences among groups in their species richness (a major component of biodiversity). For example, some animal phyla have a single described, extant species (e.g. placozoans), whereas, others have tens of thousands (e.g. annelids, molluscs, chordates) or >1 million (arthropods; [1]). Explaining this variation is a particularly exciting research area because it potentially spans and integrates most subdisciplines of biology. For example, based on recent studies (Table 1; [2–17]), differences in species richness of clades might be explained by accelerated diversification linked to changes in genomes (e.g. genome size), ecology (e.g. diet, habitat), morphology (e.g. body size), development (e.g. metamorphosis), biogeography (e.g. dispersal), or behavior (e.g. sexual selection).

In general, differences in richness among clades may be explained by two main (non-exclusive) hypotheses (Fig. 1; [19–21]). First, some clades may have more species simply because they are older (clade age hypothesis). All other things being equal, older clades will have more species because they had more time for richness to accumulate through speciation (Fig. 1A). Second, clades may accumulate species at different rates (Fig. 1B; diversification rate hypothesis). A young clade with many species will have a high net diversification rate, whereas an older clade with fewer species will have a lower net diversification rate (this must be true regardless of patterns of diversification within clades over time; Supporting Fig. S1). The net diversification rate can also be seen as the balance of speciation and extinction over time (diversification = speciation − extinction). Some authors have suggested that there is a third explanation (ecological limits on richness over time due to limited resources or carrying capacity; e.g. [22]), but this seems better considered a subset of the diversification rate hypothesis [21]. For example, new simulations show that differences in carrying capacity

Table 1. Representative studies that link variation in diversification rates among clades to specific traits (last 5 years only, not comprehensive)

Taxon	Trait	Variation explained	Reference
Vascular plants	Defense mutualisms	NA	[2]
Land plants	Rates of genome size evolution	0.34	[3]
Flowering plants	Floral traits	NA	[4]
Gall-forming midge (Insect)	Fungal symbiont	NA	[5]
Butterflies (Papilinoidea)	Plant host breadth	NA	[6]
Animal phyla	Non-marine habitat	0.30–37	[7]
Insect orders	Herbivory, wings, holometaboly	0.54–0.61	[8]
Major vertebrate clades	Terrestrial habitat	0.66–0.67	[9]
Fish	Body-size evolution	NA	[10]
Cichlid fish	Sexual dichromatism	NA	[11]
Amphibians	Tropical distribution	NA	[12]
Amphibian families	Sexual-size dimorphism	NA	[13]
Amphibian families	Climatic niche divergence	0.53	[14]
Birds (Funariidae)	Lower dispersal ability	NA	[15]
Mammals	Herbivory	NA	[16]
Mammals	Tropical distribution	NA	[17]

Studies that generated non-significant results are not shown. Only the trait (or character state) that positively impacted diversification rates is listed. Variation explained is the proportion of variation in the diversification rate among clades (based on r^2 or range of r^2 values among regression analyses) explained by the trait(s) that is presented in the cited paper. Studies listed as “NA” are those in which the variation explained was not estimated, such as those using BiSSE methods [18]. Overall, the listing here is an oversimplification of the results of each study, and readers should consult the original studies for more details.

(ecological limits) among habitats lead to differences in diversification rates, which then explain richness patterns [23]. Importantly, the only processes that can directly change the number of species in a clade are speciation and extinction, and so any other factors must act through these processes to impact clade richness.

There have been several reviews regarding the methods used for analyzing diversification rates (e.g. [20, 24, 25]). On the other hand, there have been few reviews (if any) regarding: (i) when diversification rates will explain richness patterns among clades (vs. clade ages), and (ii) what types of traits are the most important for explaining why diversification rates differ. In other words, most literature has focused on how we analyze diversification rates, rather than on whether diversification rates actually matter. Perhaps more importantly, to my knowledge, no papers have addressed which types of traits might be generally most important for explaining variation in diversification rates across the Tree of Life.

Here, I address the question: what explains patterns of species richness among clades across the Tree of Life? First, I address whether differences in richness among clades are explained primarily by differences in clade ages or diversification rates. Second, I review the factors that may explain variation in diversification rates among clades, focusing on the general types of traits that are most important (e.g. ecology vs. morphology [26]). Throughout, I will focus on case studies illustrating some of the patterns shown so far, and will emphasize how to further test these hypotheses in the future. For brevity, my review focuses primarily on extant species richness among clades of living taxa, rather than diversity over time in fossil taxa (an important and partially overlapping topic).

When are richness patterns explained by time versus diversification rates?

When trying to explain patterns of richness among clades, the most basic question is: are these differences explained by clade ages or diversification rates [19–21]? It makes little sense to test the correlates of diversification rates to understand patterns of richness among clades, if those patterns are actually explained by differences in clade ages instead. Four main studies have addressed this topic most broadly. Although these studies reached very different conclusions, they do not actually conflict strongly in their results. Overall, these results suggest that diversification rates explain richness patterns among major clades of similar rank, but with several important caveats.

Past studies: Conflicting conclusions but concordant results?

Strongly conflicting views are present in the recent literature regarding the relative importance of clade ages and diversification rates in explaining richness patterns among clades. Four main papers have addressed this question at relatively large phylogenetic scales (i.e. spanning many clades). First, McPeek & Brown [19] concluded that patterns of richness among animal clades were explained primarily by differences in clade ages and not diversification rates. They analyzed 163 species-level phylogenies from arthropods, chordates, and molluscs. They also analyzed data on richness and ages from higher taxa (e.g. orders) from select animal clades (vertebrates and insects). They found positive correlations between age and richness of clades but no significant relationships between diversification rates and richness.

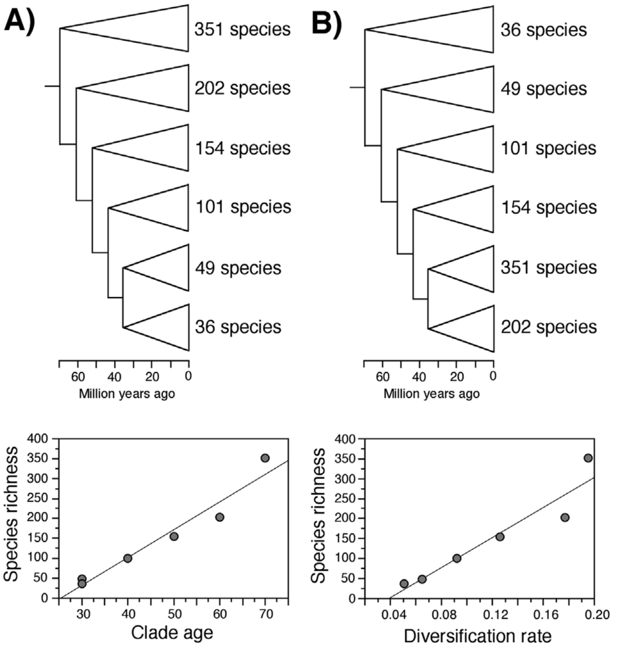

Figure 1. Hypothetical examples illustrating how differences in species richness among clades may be explained by differences in clade age or diversification rates. **A**: A case in which species richness is explained by the different ages of clades, with older clades having more species. The graph below shows the relationship between richness and clade age based on these hypothetical data. In this case, clade ages are based on the stem age of each clade (i.e. when it first split from its sister group). Triangles are all the same arbitary size, and do not indicate richness. **B**: A case in which species richness is explained by differences in net diversification rates of clades, with younger clades having faster diversification rates and more species. The graph below shows the relationship between richness and diversification rate based on these hypothetical data. Here, the diversification rate is simply based on ln(richness)/clade age, where clade age is the stem-group age of each clade.

In contrast, Rabosky et al. [27] argued that differences in richness among eukaryotic clades were not explained by clage ages or diversification rates. They examined phylogenies of many clades (e.g. families) within plants, animals, and fungi. They found few or no significant, positive relationships between age and richness of clades (contra [19]). However, they concluded that patterns of richness were not explained by diversification rates either. The logic underlying this latter conclusion is difficult to follow, since they did not test for correlations between richness and diversification rates (as in [19]). In fact, it seems to be an artifact of unrealistic simulations [28].

Hedges et al. [29] also examined a large-scale phylogeny spanning many eukaryote groups. They concluded that diversification rates were largely constant among the included clades, and that differences in richness among clades were explained largely by differences in clade ages. However, like Rabosky et al. [27], they did not actually test for relationships between richness and diversification rates of clades. They did test for correlations between richness and clade ages, but only among families and genera of mammals and birds. They found significant, positive correlations when clade ages were defined based on crown-group ages (the earliest split among living taxa within a clade) but only weak or non-significant correlations using stem-group ages (i.e. when a group first splits from its sister taxon). Yet, even crown-group ages explained relatively little variation in richness ($r = 0.43$–0.46; or <22%). Indeed, standard regression of diversification rates and richness shows that diversification rates still explain 50% of the variation in richness among mammal families and 66% among bird families (using data from [30], $\varepsilon = 0.5$, the data used by [29] for this analysis were not provided in their Supplementary Materials).

Fourth, Scholl & Wiens [30] examined relationships between species richness, clade age, and diversification across the Tree of Life (including eukaryotes, bacteria, and archaeans). They found substantial variation in diversification rates among major clades. For example, net diversification rates for plants were twice as high as in animals, and rates in animals and plants were ~10 times higher than in bacteria and archaeans (even if actual bacterial richness is many times the current number of described species). Across the Tree of Life, they found strong relationships between richness and diversification at all ranks examined (kingdoms to families), with diversification rates explaining from 41% (families), 55% (kingdoms), 64% (classes) to ~72% (orders, phyla) of the variation in richness among clades (Table 2). In contrast, there were no significant, positive relationships between richness and clade ages (using stem ages; crown ages were not used, see below). These two patterns were also found within most major clades (e.g. animals, plants, fungi, archaeans, bacteria, and major groups of protists).

Overall, these four studies differ far more in their conclusions than in their actual results. For example, only two studies [19, 30] actually tested whether diversification rates were related to richness. Importantly, most of the 163 clades considered by McPeek & Brown [19] were very young, with a median age of only 7.5 million years. In contrast, the clades examined by Scholl & Wiens [30] were older, from tens to hundreds of millions of years old (families to kingdoms). Similarly, many groups in which diversification rates have explained most (>80%) variation in richness among clades are hundreds of millions of years old (e.g. animal phyla, insect orders, major vertebrate clades, amphibians; Table 2). Thus, diversification rates seem to explain most richness patterns among major branches of the Tree of Life, even if not among very young clades.

Stems and crowns

These studies are also uniformly consistent with the idea that stem-group ages of clades may not explain richness patterns among higher-level clades. Scholl & Wiens [30] found that stem group ages did not explain richness of families and other higher taxa across the Tree of Life. Rabosky et al. [27] found similar results for animals, plants, and fungi, as did Hedges et al. [29] for families and genera of birds and mammals. McPeek & Brown [19] used crown-group ages and found strong correlations between richness and clade age, for both young clades (mostly <10 Myr) and some animal orders. Hedges et al. [29] found significant correlations between crown-group

Table 2. Representative analyses showing how much variation in species richness among clades is typically explained by variation in diversification rates

Taxon	Variation explained	Reference	Notes
Across Tree of Life			
Kingdoms ($n = 8$)	0.55	[30]	$\varepsilon = 0.5$
Phyla ($n = 71$)	0.72	“	“
Class ($n = 118$)	0.64	“	“
Order ($n = 434$)	0.72	“	“
Families ($n = 2545$)	0.41	“	“
All plants			
Class ($n = 14$)	0.87	“	“
Order ($n = 117$)	0.75	“	“
Family ($n = 682$)	0.43	“	“
All animals			
Phyla ($n = 27$)	0.81	“	“
Class ($n = 22$)	0.60	“	“
Order ($n = 203$)	0.77	“	“
Family ($n = 1710$)	0.47	“	“
Insects			
Insect orders ($n = 31$)	0.84	[8]	“
Coleoptera subfamilies ($n = 321$)	0.36	“	“
Diptera families ($n = 142$)	0.70	“	“
Hemiptera families ($n = 93$)	0.67	“	“
Hymenoptera families ($n = 77$)	0.51	“	“
Orthoptera families ($n = 26$)	0.64	“	“
Vertebrates			
Major vertebrate clades ($n = 12$)	0.86	[9]	“
Amphibian families ($n = 57$)	0.86	[14]	$\varepsilon = 0.45$
Plethodontid salamander clades ($n = 16$)	0.48–0.52	[31]	$\varepsilon = 0, 0.45, 0.9$
Phrynosomatid lizard clades ($n = 27$)	0.68	[32]	$\varepsilon = 0.45$

Note that many published analyses of diversification do not present this information, especially those using BiSSE-related methods: this explains the limited number of case studies shown. In most cases shown, diversification rates were estimated using an intermediate value of epsilon (ε, relative extinction fraction), but results were similar using alternative epsilon values. For insect orders, the tree of Rainford et al. [33] was used for consistency, since this tree was also used within the majority of insect orders (Hemiptera, Hymenoptera, Orthoptera).

ages and richness of mammalian and bird families and genera, but not stem-group ages.

Given that results from stem and crown ages can differ, which should be used? One might generally expect stem and crown-group ages to be related. However, if they are not, the use of crown-group ages could be problematic. Consider the coelacanths (Actinistia). Using crown-group ages, this clade of two species is relatively young (~5–6 Myr old; [34]). Thus, the crown-group age suggests that the low richness of coelacanths (relative to other major vertebrate clades) is explained by their “young” age. But in some ways, this would be a ridiculous conclusion. The stem age of coelacanths is >350 Myr old, and there are numerous extinct coelacanths in the fossil record [35]. Thus, the low richness of coelacanths is not simply explained by their being a “young” clade, as suggested by their crown-group age alone. Additional problems are that crown ages cannot be estimated unless multiple species are sampled within each clade (and monotypic groups cannot be included at all) and can be inaccurate with incomplete species sampling (clade ages will be underestimated). In contrast, correctly estimating stem group ages only requires sampling a single species per clade. Hedges et al. [28] considered stem-group ages to be too conservative based on their negative results for birds and mammals, but did not explain how they dealt with monotypic groups or incomplete sampling when using crown-group ages, nor whether these issues might explain the different results. Overall, this topic would benefit from further study, but there seems little basis for claiming that crown ages are always right and stem ages wrong for estimating the age-richness relationship.

Caveats and cautions: When time may matter most

An important cautionary point is that many analyses that compared the impacts of clade ages and diversification rates on richness patterns may have been strongly biased against the clade age hypothesis in their design. Specifically, many of these analyses have compared clades of the same taxonomic rank (e.g. genera, families, phyla [19, 27–30]). However, these taxa should be far more similar in their ages than if the clades that were compared were randomly selected within a given group, regardless of rank (Fig. 2; [21]). Therefore, these analyses may be strongly biased in favor of the diversification-rate hypothesis and against the clade-age hypothesis because the variation in clade ages has already been greatly reduced (e.g. if diversification rate = ln(richness)/clade age, and clade age is identical across clades, then all differences in richness should be related to diversification rates). In general, taxa of

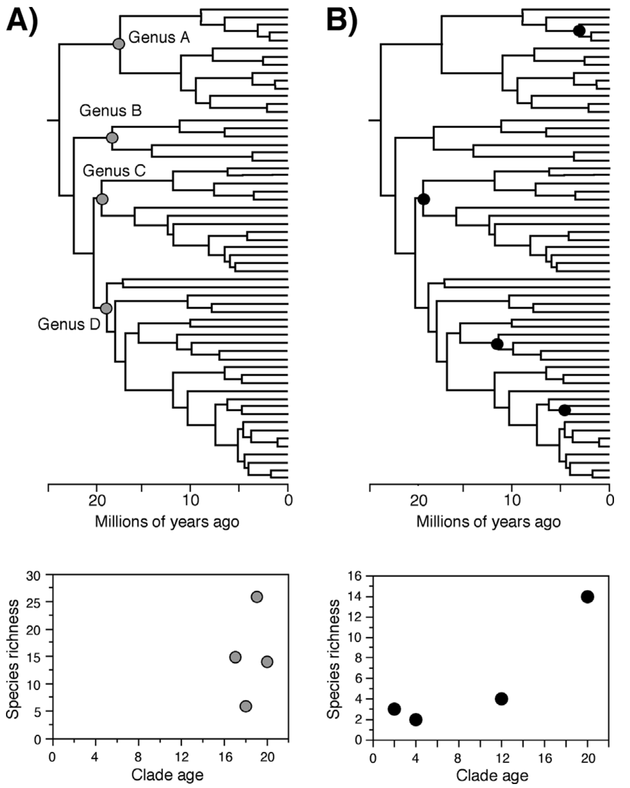

Figure 2. Hypothetical example illustrating how use of named clades of the same rank may bias tests of the relationship between clade age and richness. **A**: Four genera have similar ages despite differences in species richness, biasing the results towards showing no relationship between clade ages and species richness, and potentially showing greater importance of diversification rates in explaining richness patterns. **B**: Four arbitary points within the same phylogeny, without the constraint that the clades must be of the same taxonomic rank. In this case, the data imply a potential relationship between the ages of clades and their species richness. Whether A or B represents the correct methodological choice depends on the question. Many authors are primarily interested in comparing clades of the same rank. However, a potential bias towards similar clade ages in taxa of the same rank should be considered. Similar ages may make it less likely to find a significant relationship between clade age and richness, since one variable may show little variation. For example, biogeographic studies are not based on comparing clades of the same rank (colonization can happen at any time) and often show stronger effects of time than diversification on richness patterns among regions or habitats (see main text).

higher ranks (e.g. phyla, orders) should generally be older and more species rich than taxa of lower ranks (e.g. families, genera), simply because higher ranked taxa are composed of lower ranked taxa [30]. Thus, clade ages may be very important for explaining richness patterns when taxa of different ranks are compared [21, 30].

For example, many biogeographic studies suggest that species richness patterns among regions and habitats are explained by clade ages (i.e. regions have more species if they are colonized by older clades that colonized the region earlier), rather than differences in diversification rates of clades in different regions (e.g. [32, 36–38]). This seemingly conflicts with the studies supporting the importance of diversification rates in explaining richness patterns among clades (Table 2). This apparent conflict may be resolved by the fact that biogeographic shifts can occur at any time over the history of a group, independent of the taxonomic ranks of clades. Thus, clade ages can be far more variable in biogeographic studies than in comparisons of clades of the same rank (e.g. families). Similarly, the main analyses of McPeek & Brown ([19]; their Fig. 1) compared clades of different ranks (albeit mostly young clades), and showed a significant relationship between clade ages and richness.

An alternative (but non-exclusive) hypothesis is that clade age is more important for explaining richness patterns over shorter timescales, whereas, diversification rates become more important over longer timescales (e.g. [21–23]). For example, in young clades, stochasticity may make it less likely that clades will have the richness expected given their diversification rate [28]. Future studies should attempt to disentangle these hypotheses, especially by analyzing the relationships between richness, clade age, and diversification in younger clades (e.g. genera) and also among randomly selected clades (that can be of any age) within a given group.

Summary

In summary, there are two competing hypotheses to explain richness patterns among clades: the clade age and diversification rate hypotheses (Fig. 1). Comparisons of taxa of the same rank typically show strong relationships between diversification rates and richness (Table 2), especially when older taxa are compared (e.g. orders, phyla). Comparisons among major branches of the Tree of Life strongly suggest that diversification rates are the main explanation for differences in species richness, not clade ages. However, future studies should test whether diversification rates remain predominant in younger taxa (e.g. genera), and when clades are selected randomly within a tree. Importantly, even though clade ages may not explain differences in species richness among major clades, they may still be important for explaining some species richness patterns among regions and habitats, especially over shorter timescales [23].

Which traits are most important in explaining patterns of diversification?

Given that diversification rates seem to explain much of the variation in species richness among major clades (Table 2), what then explains this variation in diversification rates? There are now numerous studies that show significant impacts of one or more traits on diversification rates. Several recent studies are summarized in Table 1. A diagrammatic classification of different types of traits is provided in Fig. 3.

I argue that this field now needs to advance in two main ways. First, there needs to be a focus on evaluating how much variation in diversification rates is explained by each variable (e.g. from a regression of diversification rates and one or more independent variables). Many studies report significant effects of traits on diversification rates, but they do not address how much variation in diversification rates that trait explains

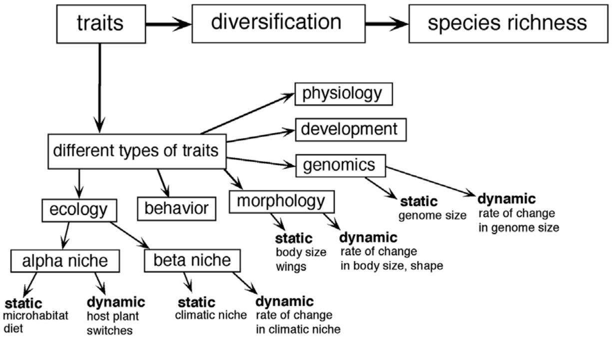

Figure 3. A diagrammatic classification of the different types of traits that can influence diversification rates and thereby drive species richness patterns among clades. Ecological traits can be classified as either relating to the alpha niche (local-scale resource use and species interactions) or the beta niche (relating to large-scale factors that influence species distributions). Furthemore, most types of traits can be classified as either static (a particular trait value or character state influences diversification) or dynamic (changes in trait values among species influence diversification). Examples of most types of traits are then given, based on those described in the text. It should be noted that many of the boundaries between these categories are fuzzy (e.g. between development and morphology or alpha and beta niche traits).

(Table 1). This is especially true for studies using BiSSE and related approaches (e.g. [18, 39]). Thus, a trait might significantly impact diversification, but the variation in diversification rates among clades that is explained might range from <5% (explaining almost nothing) to >95% (explaining almost everything). In order to understand the relative importance of different traits for explaining diversification, we need to know how much variation in diversification rates each variable explains. For example, this can be addressed by estimating diversification rates for clades, documenting the distribution of a trait (or traits) among clades, and performing a regression of the relationship between diversification and the trait(s) using phylogenetic comparative methods (e.g. phylogenetic generalized least squares; [40]).

Second, studies need to compare the relative impacts of different variables on diversification rates in the same organisms. This is needed to address the question of which types of traits are most important for explaining diversification. At present, most studies focus on testing a single predictor variable and its effects on diversification (Table 1). However, organisms are potentially impacted by multiple traits. For example, for animals, every species has a diet, body size, and climatic distribution (e.g. in tropical and/or temperate climates). Existing studies suggest that all three can influence diversification (Table 1). Importantly, an analysis might suggest that a given trait influences diversification rates, but only because that trait is partially or fully correlated (in its distribution among taxa) with a trait that directly impacts diversification rates [41]. Therefore, an analysis should consider multiple traits even if the goal is merely to test if a single trait is important.

What do we know about the relative importance of different types of traits on diversification? At present, we have only a limited set of comparisons. Below, I present some speculations about general patterns that might emerge, based on a non-comprehensive, non-systematic review of published studies. Of course, these speculations may be quickly overturned by newer studies. I merely use these to emphasize the types of comparisons that might be interesting for future studies. These unresolved questions are summarized in Table 3. I also acknowledge that there are many other ways to classify the traits discussed.

Alpha niche traits may be more important than beta-niche traits over long time scales

Many relevant traits involve ecology (Table 1), and ecological traits can be divided into those related to local-scale resource partitioning (e.g. diet, microhabitat) and those related to large-scale distribution (e.g. macrohabitat, climate). The former can be referred to as alpha niche traits (i.e. Eltonian niche; [42]) whereas, the latter can be considered beta niche traits (i.e. Grinnellian niche; [42]), following the terminology of previous studies ([43–45]). However, some traits might blur the distinction between these categories.

Recent analyses suggest that alpha niche traits (important in resource partitioning at the local scale) can be important for diversification over surprisingly deep timescales. For example, parasitism is a major driver of diversification rates among animal phyla (over a timescale of >800 million year [41]). Herbivory has a strong impact on diversification rates across insect orders (>300 million years, [8]). Across major vertebrate clades (>500 million years), most variation in diversification rates is explained by microhabitat (~67%; [9]), specifically, whether clades are predominantly aquatic (which lowers diversification rates) or terrestrial (which increases them). Importantly, many low-diversity aquatic clades are primarily tropical (e.g. coelacanths, crocodilians, lungfish), strongly suggesting that the impacts of microhabitat outweigh those of climate at this scale. This study also showed that metabolic rates had a negligible impact on diversification rates, despite the dramatic differences in metabolic rates among vertebrate clades. Across mammals, both alpha and beta niche traits are supported (i.e. diet and climatic distribution; [16, 17]), but it is difficult to address their relative impact using the BiSSE-related methods utilized.

More broadly, I speculate that traits involved in local-scale resource use (alpha niche) may be more important than those related to the broad-scale distribution of species (beta niche), as suggested in analyses across vertebrates [9]. One potential explanation for this pattern is that many alpha niche traits may change primarily over deeper timescales (e.g. aquatic fish vs. primarily terrestrial tetrapods), whereas, much variation in the beta niche may be more recent [45]. This explanation might also be used to explain deviations from this prediction. In other words, particular alpha niche traits might be less important in explaining large-scale diversification patterns if they vary primarily among closely related species. This hypothesis could potentially be tested using Pagel's [46] lambda statistic and other measures of phylogenetic signal among traits. Traits with high signal presumably vary deeper in the phylogeny, whereas, those with lower signal vary more often among more closely related species.

Table 3. Summary of unresolved questions about the relationship between traits and diversification

General questions	Specific questions
Which types of traits have the greatest impacts on diversification?	Is ecology more infuential than morphology?
	Are alpha-niche traits more influential than beta-niche traits?
	Are dynamic traits more influential than static traits?
Why would some types of traits be more important than others?	Does greater variability at shallower time scales make traits more influential for diversification at shallower time scales?
	Does less variability at deeper timescales make traits more influential at deeper timescales?
	Is there any relationship between trait variability and a trait's impact on diversification?
	Are traits with more direct mechanistic links to speciation and extinction more influential?
Is diversification more strongly influenced by speciation or extinction and when is each more important?	Are diversification patterns at shallower phylogenetic scales influenced more strongly by speciation?
	Are patterns at deeper scales influenced more strongly by extinction?
	Which types of traits primarily influence speciation versus extinction? For example, do dynamic traits primarily influence speciation?

Beta niche traits may be more important over shorter time scales

On the other hand, traits related to the beta niche may be more important for diversification over shorter timescales, especially if beta niche traits vary more among closely related species and alpha niche traits are more strongly conserved. There is evidence that the beta niche is important in explaining diversification among relatively closely related species. For example, analyses in plethodontid salamanders suggest that diversification rates among clades are strongly related to differences in rates of changes in climatic niches within these clades [31]. Clades with faster rates of climatic-niche evolution have faster diversification, suggesting that niche divergence drives diversification. A similar pattern was found among families of frogs and salamanders [14] and birds [47]. Testing the importance of climate for diversification can be relatively straightforward. However, comparing the impact of alpha and beta niche traits may be less straightforward because of the difficulty in determining exactly which alpha niche traits are most relevant for diversification in different groups.

Dynamic traits may be more important than static traits

Another way to think about traits potentially related to diversification is to classify them as either static (i.e. describing particular values of a feature, like body size) or dynamic (i.e. describing changes in a feature, like rates of change in body size). Analyses of climatic niche variables suggest that dynamic traits can be more important for diversification than static traits. For example, in plethodontid salamanders, there is a strong relationship between diversification rates and rates of change in climatic niche variables among species within those clades (i.e. a dynamic trait; [31]). In contrast, there is little or no significant relationship between diversification and mean values of climatic niche variables among species in these same clades (i.e. a static trait; [37]). Similarly, across amphibian families [14], there is a strong relationship between climatic niche divergence within families (dynamic trait) and rates of diversification, but only a weak relationship between diversification and static values of climatic variables (e.g. whether families occur in high or low precipitation regions). In plants [3], there is no relationship between speciation rates and genome sizes (static), but a strong relationship between rates of genome size evolution and speciation (dynamic).

Why might dynamic traits be more influential on diversification than static traits? One potential explanation is that with dynamic traits, there can be a relatively straightforward mechanistic relationship with speciation, whereas, this can be more ambiguous with static traits. For example, it is clear that climatic niche divergence can potentially drive speciation, especially if an incipient species occurs under climatic conditions that its sister species cannot tolerate (e.g. [48–50]). In contrast, it remains unclear why warmer climates should drive faster diversification: some other hypothesis or mechanism must be invoked to directly link warmer climates to diversification. Turning to the genome size example [3], it is well known that the acquisition of polyploidy can drive speciation in plants (dynamic trait), but once polyploidy is acquired (static trait), polyploid lineages do not appear to have higher speciation or diversification rates [51, 52]. Simply being polyploid is not a mechanism of speciation.

This dichotomy between traits that have direct or indirect effects on diversification could potentially apply to many different characteristics. I speculate that traits with more direct effects on diversification may be more important in explaining richness patterns.

Finally, I note that the distinction between static and dynamic might be somewhat fuzzy in some cases. For example, herbivory in insects can be treated as a static trait that increases diversification rates (e.g. [8]). However, the reason why herbivory promotes diversification may be because shifts between different host plant species drives speciation in herbivorous insects (e.g. [6]). These changes in host plants could be considered a dynamic trait. A similar explanation might apply to terrestrial microhabitat among major vertebrate clades, a seemingly static trait with a strong impact on diversification [9], which might promote dynamic divergence in microhabitat.

Ecology may be more important than morphology

I speculate that ecology might often be more important for explaining diversification patterns than morphological traits. This speculation is based on the idea that ecology may have more direct impacts on diversification than morphology (whereas morphology might be important primarily because it is linked to ecology).

There is some support for this idea. In an analysis among bird families, the most important variables for predicting diversification were the propensity for annual dispersal and a generalist diet, whereas, morphological variables such as body size and sexual dichromatism had weaker or non-significant effects [53]. Analyses in plethodontid salamanders showed that ecology (rate of climatic niche divergence [31]) is more important than rates of change in morphology (size and shape [54]) in explaining variation in diversification rates among clades. Furthermore, rates of change in these morphological variables and in climatic niches were uncorrelated [55], and morphology is largely uncoupled from microhabitat [56]. Similarly, across vertebrates, ecology (aquatic vs. terrestrial habitat use) explains most variation in diversification rates among the major clades (~67%; [9]). Thus, there may be little remaining variation for morphology to explain, and low diversification rates in aquatic clades are largely consistent across a dramatic range of body sizes and shapes. For example, diversification rates are relatively low in both aquatic crocodilians (large size, four limbs) and aquatic lampreys and hagfish (relatively small, with no jaws, limbs, or paired fins; [35]). Among animal phyla [41], most variation in diversification rates (~67%) is explained by only three variables, two ecological (parasitism, habitat) and one morphological (a skeleton).

There is also support for the importance of morphology in other studies, but not necessarily to the exclusion of ecology. In a recent study of flowering plants, flower morphology appeared to strongly influence diversification [4], but ecological traits were not tested, and the importance of floral traits in speciaiton may depend on their role in mediating interactions between plants and pollinators (i.e. ecology). Across insect orders, the positive impacts of two morphological traits (wings, complete metamorphosis) on diversification were similar to those of herbivory, but only herbivory was consistently supported across different trees [8]. Among amphibian families, both sexual-size dimorphism [13] and climatic-niche divergence [14] seem to impact diversification rates. Other studies have found positive relationships between diversification and morphology, such as a study of rates of body-size evolution in fishes [10]. However, that study did not include ecological variables. If body size is strongly related to ecology, changes in body size may simply be correlated with changes in ecology (e.g. microhabitat and/or diet), and body size itself might have little unique importance to diversification. In general, changes in morphology may often accompany changes in ecology [57–59]. What is ultimately needed is a mechanistic understanding of how traits are related to diversification, to decipher which traits are most important and why.

Extinction may be more important than speciation for explaining large-scale diversification and richness patterns among clades

Ultimately, we want to understand patterns of diversification and richness in terms of how each trait influences the rates and processes of speciation and extinction. The net diversification rate of a clade can be defined as the rate of speciation minus the rate of extinction [20, 60]. Many studies that analyzed the correlates of diversification used methods for estimating diversification rates (e.g. [60]) that do not distinguish the contributions of speciation and extinction to overall variation in diversification rates (e.g. [7–9]). Distinguishing the contributions of these processes may require relatively large and complete phylogenies (e.g. using BiSSE-type methods; [18, 61]), which are not always available.

Furthermore, it is unclear how well different estimators of speciation and extinction rates will perform with incomplete species sampling and heterogeneity of rates within clades (which are not necessarily problematic for estimating net diversification rates, at least using stem ages). Some methods may perform poorly at estimating extinction and speciation rates (e.g. BAMM; [62, 63]).

Even with limited information about these rates, I speculate that extinction may play a much greater role than speciation in driving many patterns of net diversification and richness at larger phylogenetic scales. For example, some of the most striking patterns of species richness involve clades that are hundreds of millions of years old, in which some taxa have thousands of species and others have only one or a handful of living species. In many of these cases, it is clear that the low richness of these taxa is not explained by a failure to speciate over tens or hundreds of millions of years. Instead, they have rich fossil records that show that their current richness is only a fraction of their richness in the past (e.g. coelacanths, lungfish, rhyncocephalian reptiles; [35]). Thus, their current richness seems to have been strongly impacted by extinction.

In general, we know little about the relative contribution of differences in rates of speciation and extinction to patterns of diversification and species richness among clades. Thus, we know little about how the relative contribution of each process to diversification might change with phylogenetic scale (e.g. does extinction become more important over deeper time scales?) and with different traits that significantly impact diversification (e.g. do dynamic traits influence diversification primarily through increasing speciation rates?). These should be important questions for future research (Table 3).

In a similar vein, many factors discussed here focus (either explicitly or implicitly) on driving diversification through accelerating speciation (e.g. climatic niche divergence). The factors that drive extinction may be quite distinct and also important. For example, occurrence in marine environments has a strong, negative impact on net diversification rates of animal phyla [7, 41], and may do so by increasing extinction. Indeed, within many vertebrate clades, the marine taxa living today replaced earlier marine lineages within these groups that went extinct. This includes mammals, birds, crocodilians, turtles, lizards, and snakes [64], and remarkably, the most diverse group of fish (ray-finned fish, actinopterygians [65]).

Species interactions may be broadly important

Studies on diversification suggest that species interactions can be important in many ways. First, positive interactions between species can accelerate diversification. For example, defense mutualisms increase diversification rates in plants [2]. Similarly, the origins of a symbiosis between a fungus and a gall-inducing insect (midge; Diptera) have accelerated diversification in lineages with fungi relative to those without [5].

Negative interactions are also important. For example, herbivory and parasitism are important for diversification across clades that include the majority of described species (herbivory in insects [8], parasitism across animals [41]).

Perhaps the most universally important negative interaction is competition. A key component of the ecological theory of adaptive radiation is that diversification within a clade is accelerated when competition with other clades is reduced (i.e. ecological opportunity; [58]). For example, analyses in plethodontid salamanders [31] and hylid frogs [36] show accelerated diversification in clades that have little or no geographic overlap with other clades in their families. Similarly, “key innovations” are traits that are thought to reduce competition by allowing utilization of novel resources and thereby accelerate diversification, another key aspect of adaptive radiation [58]. Thus, many traits that drive diversification may ultimately be related to competition.

There is also an extensive literature suggesting that diversification rates seem to slow within clades over time, a pattern often attributed to competition (review in [66]). But what this pattern means (and whether it is real or artifactual) is unclear [66]. Studies that link slowing diversification within clades over time to ecological data relevant to competition (such as overlap between species in geographic space and resource use) remain uncommon [66]. Furthermore, if most clades show this pattern of slowing diversification over time, then the presence of this pattern may actually have very little value for explaining diversification, species richness, and trait evolution (e.g. [31, 55]).

In general, species interactions may be extremely important in driving diversification. However, rather than being a competing explanation relative to other traits, species interactions may be the mechanism that underlies the importance of many traits to diversification (e.g. any novel trait that changes resource utilization might spur diversification by reducing the constraining effects of competition; [58]). Nevertheless, an important unresolved question is the relative importance of positive and negative species interactions for explaining patterns of diversification.

Conclusions and outlook

In this review, I highlight recent advances in understanding the causes of the dramatic differences in species richness across branches of the Tree of Life. Two main hypotheses to explain these differences are the clade age and diversification rate hypotheses. Recent studies show that when comparing clades of similar rank (e.g. families, phyla), differences in diversification rates seem to generally explain patterns of species richness, at least for older clades. Differences in clade ages may be more important for explaining richness patterns when the clades compared can be of any rank or age. The primary challenge for understanding richness patterns among major clades (of similar age or rank) is to reveal the traits that explain variation in diversification rates. To make progress in this area, it is crucial for future studies to compare the impacts of multiple traits on diversification, and to evaluate how much variation in diversification rates each trait explains (rather than simply testing for significant effects of a single variable). Future studies should not only test particular traits, but should seek to understand which general types of traits are most important (e.g. alpha vs. beta niche traits, dynamic vs. static traits, ecology vs. morphology). The relative importance of different traits (and types of traits) may depend on the phylogenetic scale considered, patterns of variability in the traits at the scale considered, and whether traits are directly linked to mechanisms of diversification or not (i.e. speciation and extinction). The relative contributions of speciation and extinction dynamics to diversification (and how this changes with different timescales and traits) also remains unresolved. Overall, relating the remarkable diversity of life in terms of traits (e.g. morphology, behavior, ecology, physiology, genomics) to the dramatic variation in species richness among clades will be difficult, but may be one of biology’s great endeavors.

Acknowledgment
I thank Andrew Moore for inviting me to submit a paper on this topic, and anonymous reviewers for helpful comments that improved the paper.

The author has declared no conflicts of interest.

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