

Trait-based species richness: ecology and macroevolution

John J. Wiens* 

Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721-0088, USA

ABSTRACT

Understanding the origins of species richness patterns is a fundamental goal in ecology and evolutionary biology. Much research has focused on explaining two kinds of species richness patterns: (i) spatial species richness patterns (e.g. the latitudinal diversity gradient), and (ii) clade-based species richness patterns (e.g. the predominance of angiosperm species among plants). Here, I highlight a third kind of richness pattern: trait-based species richness (e.g. the number of species with each state of a character, such as diet or body size). Trait-based richness patterns are relevant to many topics in ecology and evolution, from ecosystem function to adaptive radiation to the paradox of sex. Although many studies have described particular trait-based richness patterns, the origins of these patterns remain far less understood, and trait-based richness has not been emphasised as a general category of richness patterns. Here, I describe a conceptual framework for how trait-based richness patterns arise compared to other richness patterns. A systematic review suggests that trait-based richness patterns are most often explained by when each state originates within a group (i.e. older states generally have higher richness), and not by differences in transition rates among states or faster diversification of species with certain states. This latter result contrasts with the widespread emphasis on diversification rates in species-richness research. I show that many recent studies of spatial richness patterns are actually studies of trait-based richness patterns, potentially confounding the causes of these patterns. Finally, I describe a plethora of unanswered questions related to trait-based richness patterns.

Key words: adaptive radiation, diversification, macroecology, macroevolution, species richness, trait.

CONTENTS

I. Introduction	1366
II. Why care about trait-based richness?	1368
III. The causes of species richness patterns	1369
IV. Ultimate causes of trait-based richness patterns	1370
V. How do we infer the direct causes of trait-based richness patterns?	1372
VI. What is known about the causes of trait-based richness patterns?	1373
VII. Adding complexity	1374
VIII. The problem of ignoring trait-based richness	1377
IX. Unanswered questions	1380
(1) Are diversification rates overrated?	1380
(2) Why are transition rates not transformative?	1380
(3) Are there generalities underlying all three types of richness patterns?	1380
(4) What are the most important ‘ultimate’ causes of trait-based richness patterns?	1381
(5) Do communities, regions, or clades ‘fill up’ with species having similar traits?	1381
(6) Do parallel adaptive radiations in different locations generate parallel patterns of trait-based richness?	1381
(7) Will studying the origins of trait-based richness patterns help reveal the causes of other richness patterns?	1383
(8) Are trait-based richness patterns relevant to other questions?	1383

* Author for correspondence (Tel.: +520 621 0337; E-mail: wiensj@arizona.edu).

X. Conclusions	1383
XI. Acknowledgements	1384
XII. References	1384
XIII. Supporting information	1387

I. INTRODUCTION

A fundamental goal of ecology and evolutionary biology is to explain patterns of **species richness** (see Glossary in

Table 1 for definitions of boldfaced terms). Most papers on species richness focus on explaining one of two kinds of patterns. First, countless studies address **spatial richness patterns**, such as the presence of more species in the tropics

Table 1. Glossary.

Ancestral state	The character state inferred to be present at a given node or branch of a phylogeny.
Carrying capacity	The number of species that a given location, clade, or state can support given competition for finite resources. Limited carrying capacity (or ‘ecological limits’) is sometimes considered to be an explanation for species richness patterns.
Character	Another word for ‘trait’: a feature that can take different forms or values among species (i.e. different states).
Clade-based richness patterns	Differences in species numbers among groups of organisms (presumably clades). For example, there are far more species of arthropods than of other animal phyla.
Diversification rate	The rate of accumulation of species over time within a clade, or the speciation rate minus the extinction rate.
Diversification rate hypothesis	In the context of trait-based richness patterns, this hypothesis posits that more species have a given state because species with that state have increased rates of species accumulation (diversification) relative to species without that state.
Ecological opportunity	A release from ecological constraints that can provide new potential for diversification in a group of organisms. These constraints might be released by dispersal to a new area, a key innovation that makes novel resources available, or the extinction of competitors or other antagonists (Yoder <i>et al.</i> , 2010).
Ecological speciation	The process by which reproductive isolation evolves between incipient species as a result of ecologically based divergent selection (e.g. Schluter, 2000; Nosil, 2012).
Spatial richness patterns	Differences in species numbers among locations. These different locations might include different local communities, different elevations, or different large-scale geographic regions.
Species richness	The number of species. Species numbers can vary among locations (spatial richness), among groups of organisms (clade-based), and among different states or values of a trait (trait-based).
State	Each alternative form of a given character or trait; for example, the states for the character ‘diet’ might include herbivory, omnivory, and carnivory.
State-dependent speciation–extinction (SSE) models	A group of maximum-likelihood models designed to estimate rates of speciation and extinction associated with each state of a character. These models can also be used to estimate transition rates among states, and ancestral states at each node of a phylogeny. Importantly, unlike most other methods, SSE methods can incorporate the effects of different diversification rates in each state on the estimation of transition rates and ancestral states.
Time-calibrated phylogeny	An evolutionary tree in which the estimated lengths of the branches reflect time (e.g. species pairs separated by shorter branches split from each other more recently). These trees can be used to estimate rates of diversification for each state, the rates of transitions between different states, and how long ago each state originated.
Trait	A given ecological or phenotypic variable, which can take different values among species (i.e. a character with different states). ‘Trait’ is also sometimes used synonymously with ‘state’.
Trait age hypothesis	In the context of trait-based richness patterns, this hypothesis postulates that there are more species that have a given state because that state has been present within the group of organisms longer than other states (originated earlier), and so has had more time to accumulate species through speciation.
Trait-based richness	The number of species with each state or value of a given character (trait) or characters.
Trait origin hypothesis	In the context of trait-based richness patterns, this hypothesis postulates that more species have a state because that state evolved more frequently than other states. By originating more frequently, the state can potentially become more common even if it arose after other states and even if it is not associated with a faster diversification rate.
Trait space	The set of values of a given ecological or phenotypic variable or variables among a set of species.
Transition rate	The expected number of changes between two character states per unit time. A state may be more common in a group of species because that state has a high rate of origin.

than in temperate regions (e.g. Pianka, 1966; Hillebrand, 2004; Mittelbach *et al.*, 2007; Brown, 2014; Fine, 2015). Second, a smaller set of studies focus on **clade-based richness patterns** (e.g. Scotland & Sanderson, 2004; McPeck & Brown, 2007; Wiens, 2017), such as why some groups have more species than others (e.g. why are most animal species insects and why are most plants angiosperms?).

Here, I highlight the origins of a third kind of richness pattern: species richness in **trait space** (Fig. 1). A **trait** is a given ecological or phenotypic variable, which can take different values among species (i.e. a **character** with different **states**). Trait space is the set of values of this variable among a set of species. The trait space might include different mean body sizes among species in a bird family, different states of a more-or-less discrete ecological character (e.g. diet, habitat), or the set of values for multiple continuous variables. Species richness in trait space (**trait-based richness**) is the number of species with each state or value of a given character(s). The character and states could describe any ecological, phenotypic, or evolutionary trait of interest, such as body size, ploidy level, microhabitat, or reproductive mode. As one example, think of diet in animals as a trait with different states (e.g. herbivory, carnivory, omnivory). A given group of animals might have many carnivorous species, fewer omnivorous species, and even fewer herbivorous species.

These patterns of trait-based richness might differ across clades, habitats, and communities (Kratina *et al.*, 2012; Román-Palacios, Scholl & Wiens, 2019). But how do such patterns arise?

I suggest here that explaining the origins of these trait-based richness patterns is an underexplored field that lies at the intersection of ecology and macroevolution. Spatial richness patterns are a long-standing focus of ecological research (e.g. Pianka, 1966; Mittelbach *et al.*, 2007; Brown, 2014; Fine, 2015). In recent decades, there has also been burgeoning interest in functional traits in ecology (e.g. McGill *et al.*, 2006; Messier, McGill & Lechowiz, 2010; Violle *et al.*, 2014; Levine, 2016). But the field of trait-based ecology has not generally focused on the species richness associated with different states or trait values, and especially not on how these trait-associated richness patterns arise. This neglect might occur because fully understanding the origins of trait-based richness patterns requires incorporating macroevolutionary explanations, such as when and how often each state arises, and whether species with a given state become more frequent through increased rates of species proliferation (**diversification**). Most trait-based ecologists may not typically focus on macroevolutionary questions or methods.

Some trait-based species richness patterns have traditionally received considerable attention in ecology, such as the

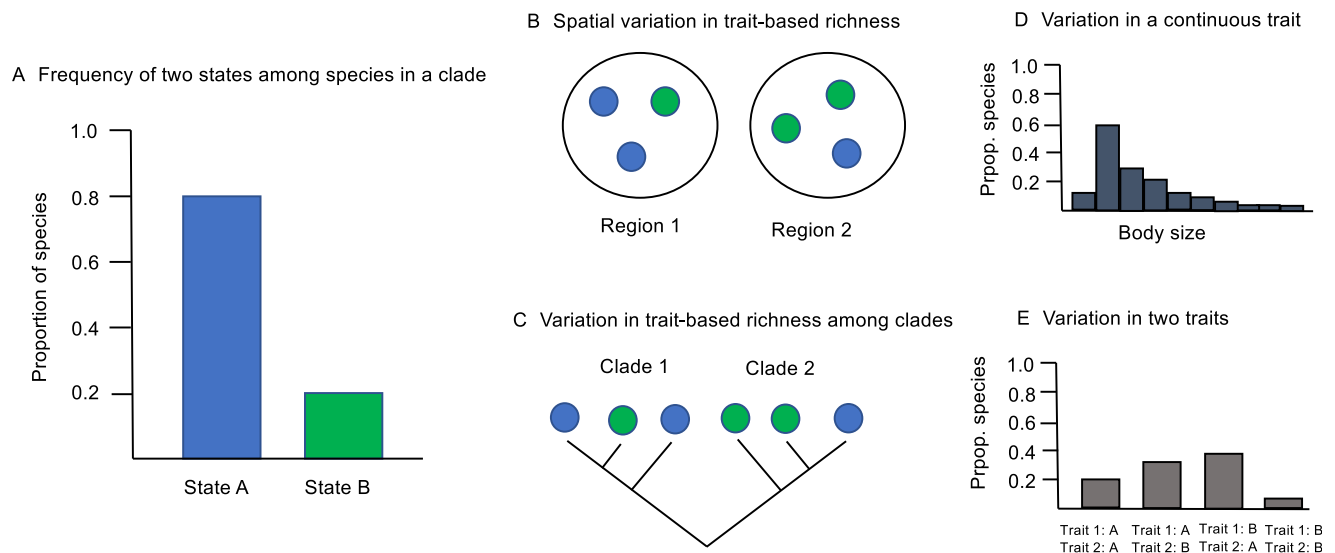


Fig. 1. Patterns of trait-based species richness. (A) The simplest case is a single trait with two discrete states in a clade. In this hypothetical example, 80% of the species have state A, and 20% have state B. The main focus of this review is to address how such trait-based richness patterns come about. Other patterns of trait-based species richness are possible. (B) Spatial variation in trait-based richness. In this example, a trait with two states (state A = blue, state B = green) varies among regions in its frequency among species, with 67% of the species in region 1 having state A and only 33% in region 2. (C) Trait-based richness can also vary among clades. Here, a trait with two states (A = blue, B = green) varies in its frequency among species in each of two clades, with 67% of the species in clade 1 having state A and only 33% in clade 2. (D) The examples in A–C all involve traits with two alternative, discrete states. There can also be trait-based richness in continuous characters, such as the distribution of body sizes among species. (E) One can also consider trait-based richness in two or more traits simultaneously. Here, there are two traits (1 and 2), each with two states (A and B). In this hypothetical clade, there is a different proportion of species with each combination of the four possible combinations of states for the two characters.

distribution of different body sizes among species within a group of organisms (e.g. Hutchinson & MacArthur, 1959; Maurer & Brown, 1988; Blackburn & Gaston, 1994; Jones & Purvis, 1997; Kozłowski & Gawelczyk, 2002). These body-size distributions are a classic topic in macroecology (Brown & Maurer, 1989; Gaston & Blackburn, 2000) and an obvious pattern of trait-based species richness. However, far fewer studies have explored how these size-related richness patterns originate through macroevolutionary processes, such as rates of body-size evolution and different diversification rates associated with different body sizes (e.g. Maurer, Brown & Rusler, 1992; Kozłowski & Gawelczyk, 2002).

By contrast, trait evolution and trait-related diversification are major topics in macroevolution. Numerous macroevolutionary studies use phylogenies to address how many times a given character state has evolved (Losos *et al.*, 1998; Ord & Cooke, 2016; Furness *et al.*, 2021), what variables might be correlated with the evolution of that state (Goodwillie *et al.*, 2010; Zanne *et al.*, 2014; Furness *et al.*, 2021), and whether or not that state has promoted rapid species diversification (Price *et al.*, 2012; Weber & Agrawal, 2014; Nakov, Beaulieu & Alverson, 2019). There is also macroevolutionary research on trends in trait values over time in the fossil record [e.g. Cope's rule of increasing body size (Jablonski, 1997; Heim *et al.*, 2015)]. Yet, far fewer evolutionary studies focus specifically on explaining the species richness associated with different trait values (e.g. why do more species have state A than state B?), and on testing the different possible explanations for such patterns.

Some evolutionary questions are focused on trait-based species richness patterns. For example, the preponderance of sexual reproduction among species, despite its costs, is a long-standing evolutionary puzzle known as the 'paradox of sex' (Williams, 1975; Maynard Smith, 1978; Bell, 1982; Otto & Lenormand, 2002; Neiman, Lively & Meirmans, 2017; Burke & Bonduriansky, 2017). This is actually a question about trait-based richness (i.e. why do more species have sexual reproduction than asexual reproduction?). Yet this question has mostly been addressed from a within-population perspective (Otto & Lenormand, 2002; Neiman *et al.*, 2017), rather than from a macroevolutionary perspective, with some exceptions (e.g. Fontaneto *et al.*, 2012; Chen & Wiens, 2021; Moreira, Fonseca & Rojas, 2021). Further, this richness pattern is often simply assumed rather than being explicitly estimated, and the pattern is not always so clear when one does try to estimate it (e.g. Chen & Wiens, 2021).

In summary, many ecological studies have addressed trait-based richness patterns, but generally without analysing the macroevolutionary processes that generate these patterns (i.e. diversification, trait evolution). At the same time, numerous evolutionary studies have analysed these same macroevolutionary processes, but generally without focusing on explaining trait-based richness patterns.

Most importantly, despite intriguing case studies on particular traits in certain organisms (e.g. Burin *et al.*, 2016;

O'Meara *et al.*, 2016), there has been little focus on the causes of trait-based richness patterns as a general question. Thus, a broader conceptual framework is lacking to explain these patterns that spans all taxa and traits. As one example of this neglect, a recent review listed 25 unanswered questions at the intersection of macroecology and macroevolution (McGill *et al.*, 2019). The origins of trait-based richness patterns clearly lie at this intersection, but this topic was not among these questions.

Some might argue that it is better to focus only on specific causes of richness patterns in specific traits rather than on broad explanations for trait-based richness, given the potential diversity of traits across organisms (e.g. body size, sexual reproduction, diet, habitat). Yet, this view is contrary to the search for general underlying principles in ecology, evolutionary biology, and in science overall. Furthermore, it can be beneficial to think about the origins of trait-based richness patterns in general in comparison to other types of richness patterns (i.e. spatial, clade-based) to seek a more comprehensive understanding of how richness patterns arise.

Here, I highlight these trait-based species richness patterns and how they originate. I outline the general causes of trait-based richness patterns, in comparison to spatial and clade-based species richness patterns. I then address how we can study these causes, and what is known about these causes from a survey of recent case studies. I initially focus on simple examples and case studies that involve a single variable with two discrete states in a single clade (Fig. 1A). I later outline more complex scenarios (Fig. 1B–E), involving continuous characters and patterns among clades, regions, and multiple traits. I next address how studies of spatial species richness have sometimes been confounded with trait-based richness, potentially leading to erroneous conclusions about the origins of spatial richness patterns. Finally, I describe many unanswered questions related to trait-based richness patterns and their origins, and their relationship to other richness patterns. However, before addressing any of these topics, I first address a more basic question: why should anyone care about trait-based richness patterns in the first place?

II. WHY CARE ABOUT TRAIT-BASED RICHNESS?

My goal in this paper is to provide a general framework to address how trait-based species richness patterns arise: it is not to suggest that no one has studied any trait-based richness patterns before. In some ways, ecologists and evolutionary biologists are already interested in trait-based richness patterns, such as body-size distributions and the paradox of sex (see Introduction, Section I). These two patterns are specific examples of a broader type of richness pattern (trait-based richness) that can be distinct from spatial richness and clade-based richness. At the same time, I acknowledge that some readers may not be convinced that these trait-based richness patterns are interesting.

Trait-based richness patterns are interesting and important because traits are (Fig. 2). Traits can describe what species do (e.g. diet, reproductive mode), where they live (e.g. microhabitat), when they are active (e.g. nocturnal), how they interact (e.g. as hosts, predators, prey, parasites, mutualists), their function in communities and ecosystems, and whether a given pair or group of species are likely to compete or not (among other things). Therefore, even if one is not interested in trait-based species richness *per se*, the number of species with each trait or set of traits (in a clade, community, ecosystem, or region) should be important to many of the most fundamental questions in ecology and evolutionary biology (Fig. 2).

As one example, the relationship between species richness and ecosystem function has been a major topic in ecology for decades (e.g. Tilman *et al.*, 1997; Loreau *et al.*, 2001; Hooper *et al.*, 2005; Naeem, Duffy & Zavaleta, 2012). In a classic study of experimental grassland plots, Tilman *et al.* (1997) manipulated plant species richness, the number of functional groups present (e.g. nitrogen-fixing legumes, C₄ grasses), and the number of species in each functional group, and then measured the effects of these manipulations on ecosystem processes (e.g. biomass production). They found that species richness was not as important for ecosystem function as the presence of species from many functional groups. In some ways, this seems obvious: ecosystem function depends on species' traits. Therefore, the number of co-occurring species with each trait (trait-based richness) should matter more for ecosystem function than the simple number of species alone (e.g. Loreau *et al.*, 2001).

Similarly, among evolutionary biologists, there has been intense interest for decades in adaptive radiation (e.g. Schluter, 2000; Glor, 2010; Gillespie *et al.*, 2020). These radiations are often thought to begin when certain niches (ecological resources or roles, in this context) are unoccupied and they end or slow down as these niches fill up with species over time (Schluter, 2000; Yoder *et al.*, 2010; Stroud & Losos, 2016). Given this view, the process of adaptive radiation should be determined by the number of species occupying each niche at each point in time, and the occupation of a niche should depend on species' traits. Therefore, adaptive radiation should be intimately related to trait-based species richness. However, few authors (if any) have explicitly

analysed trait-based richness patterns to study adaptive radiation.

Ecosystem function and adaptive radiation are just two additional examples of why trait-based richness patterns matter. In Sections VIII and IX, I describe potential pitfalls of ignoring trait-based richness, and some of the many unanswered questions related to trait-based richness patterns (including many additional types and applications of trait-based richness patterns; Fig. 2). Nevertheless, my main focus herein is on how these trait-based richness patterns arise.

III. THE CAUSES OF SPECIES RICHNESS PATTERNS

The three general types of richness patterns (spatial, clade-based, trait-based) each have a set of causes that partially overlap. I describe the direct causes of each of these types of patterns in order below.

Spatial richness patterns are directly determined by speciation, extinction, and dispersal (Ricklefs, 1987). These are the only processes that actually change the number of species in a given location. Therefore, differences in richness among locations (e.g. different communities, habitats, elevations, latitudes, or regions) must involve differences in the rates and patterns of these processes among locations. These rates and patterns of speciation, extinction, and dispersal are often summarised and analysed as three non-exclusive factors that determine richness: (i) diversification rates; (ii) dispersal frequency; and (iii) the relative timing of successful colonisation among locations (Ricklefs, 2006; Li & Wiens, 2019). First, species richness may be higher in some locations because conditions there (e.g. climate) increase net diversification rates in the lineages present, where diversification is the net rate of species accumulation over time, or the rate of speciation minus the rate of extinction (Ricklefs, 2006). Since this hypothesis relates to the balance of speciation and extinction over time, it includes the extreme case when extinction (local or global) eliminates a species from a given location (i.e. diversification is not simply speciation, but also includes extinction). Alternatively, some locations may have higher or lower richness because they receive more or fewer

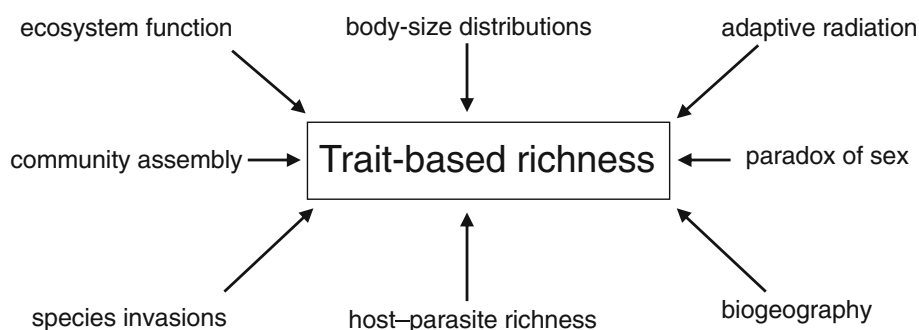


Fig. 2. Diagram illustrating some of the topics in ecology and evolutionary biology that are related to trait-based richness.

colonists from other regions (dispersal rate; MacArthur & Wilson, 1967). Finally, a location may have higher richness because it was successfully colonised before other locations, potentially allowing more time for richness to build up in that location through *in-situ* speciation (Stephens & Wiens, 2003; Ricklefs, 2006). By ‘successful colonisation’ I mean a colonisation that left descendants that survive to the present day (colonisations that did not leave present-day descendants do not contribute to present-day richness patterns). Of course, spatial richness patterns may be strongly related to many other factors (e.g. area, climate, productivity, competition), and these factors might reasonably be considered the ultimate causes of these richness patterns (as opposed to the proximate causes). Yet, these other factors must act on the processes of speciation, extinction, and/or dispersal in order to impact richness patterns (Ricklefs, 2006).

Clade-based richness patterns have somewhat simpler explanations. Certain clades may have more extant species than others because they: (i) have faster rates of diversification; and/or (ii) because they are older (e.g. McPeck & Brown, 2007). Clades with faster diversification rates will accumulate species more rapidly. Older clades can potentially have more time to accumulate richness through speciation, even without a faster rate of diversification. Clearly, there is no dispersal of species between clades. Various factors may then influence a clade’s diversification rate, including different types of ecological, genomic, and phenotypic traits (review in Wiens, 2017).

We can now compare how trait-based richness patterns arise relative to these two other types. We start with the simplest case: a group of organisms in which different species have different states of a given character (Fig. 1A). The number of species with each state will depend directly on the diversification rate of the species with each state, the rate of transitions among states, and the amount of time that each state is present among extant lineages. We can describe these non-exclusive hypotheses as the: (i) diversification rate hypothesis; (ii) trait origins hypothesis; and (iii) trait age hypothesis (Table 1, Fig. 3). First, a state may have a higher frequency among species because it is associated with faster rates of diversification than other states, leading to more rapid proliferation of species with this state over time. Second, a state may be present in more species because it originates more frequently (i.e. more transitions to this state from other states) and/or is lost less frequently (i.e. fewer transitions to another state). Third, a state may be more frequent among species because it evolved earlier in the history of the group than other states, allowing more time for species with this state to accumulate over time through speciation. Note that these three hypotheses focus on clades and trait origins that have survived to contribute to present-day richness patterns.

These three hypotheses for trait-based richness patterns (Fig. 3) have clear parallels to the hypotheses underlying spatial richness patterns and clade-based richness patterns. All three types of richness patterns have a hypothesis related to diversification rates, and all three have one related to time

(either the amount of time in a location, the time of origin of a clade, or the time of origin of a character state). Spatial and trait-based patterns also have a hypothesis related to the frequency of transitions, either through dispersal (spatial), or through character evolution (trait-based).

Of course, these three hypotheses do not explain all the ecological and evolutionary factors underlying trait-based richness patterns (see Section IV). Nevertheless, these hypotheses should be a crucial starting point. Most importantly, alternative factors that underlie trait-based richness patterns must act through diversification rates, transition rates, and the time spent in each state, in order to impact the richness associated with each state. Therefore, I consider these three hypotheses to be the ‘direct’ or ‘proximate’ causes of trait-based richness patterns, as opposed to the ‘ultimate’ cause (Fig. 4). The ultimate causes could also be referred to as ‘primary’ causes (i.e. if one starts with the causes and then moves towards the richness patterns instead of starting with the observed richness patterns first and moving towards the causes).

Along these lines, some authors have considered limited carrying capacity to be an alternative to the time and diversification rate hypotheses, at least for spatial richness patterns (e.g. see Fig. 1 in Mittelbach *et al.*, 2007). Although carrying capacity might be important (but see Harmon & Harrison, 2015), it represents a different level of explanation (like climate). Thus, carrying capacity can only influence richness by influencing speciation, extinction, and dispersal (or transition rates for trait-based richness). For example, even if limited carrying capacity did constrain the richness of a region, clade, or character state to only 10 species, there will never be 10 species without speciation and/or dispersal (or transitions for trait-based richness). Carrying capacity is not a process that generates or eliminates species: speciation and extinction are. Furthermore, the presence of limited carrying capacity does not invalidate the diversification rate hypothesis: simulations show that even when habitats vary primarily in carrying capacity, variation in species richness is still strongly related to variation in diversification rates (Pontarp & Wiens, 2017). Again, carrying capacity influences richness through its impacts on diversification and successful dispersal.

IV. ULTIMATE CAUSES OF TRAIT-BASED RICHNESS PATTERNS

The three hypotheses described above (Fig. 3) offer one level of explanation for trait-based richness patterns. Another level of explanation is to understand the ecological and evolutionary factors that underlie these hypotheses (Fig. 4). These might include factors below the species level (e.g. microevolution) and above (e.g. communities, biogeographic regions). For example, each origin of a state may depend on mutation, the developmental processes that generate the phenotype, and natural selection that helps

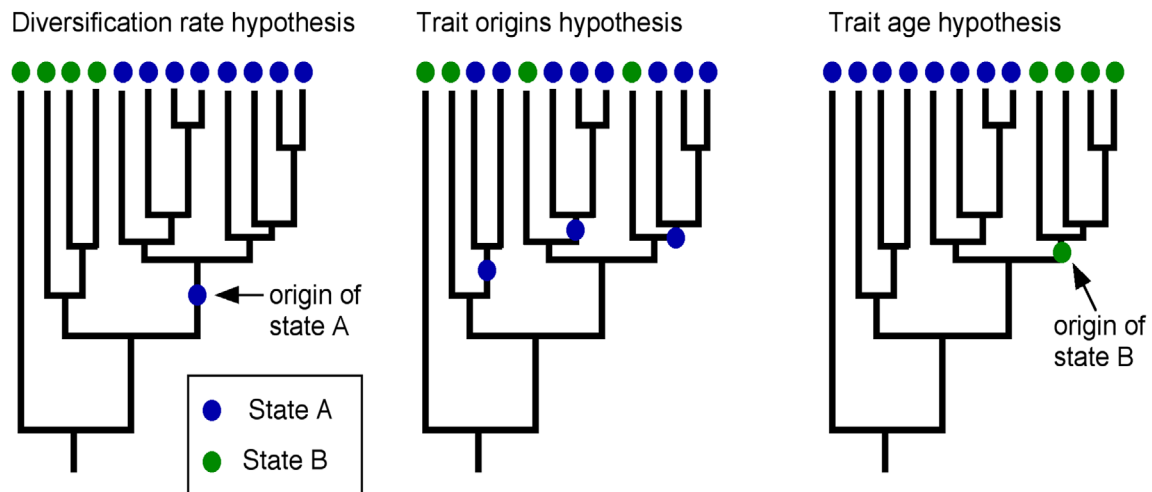


Fig. 3. The three main hypotheses to explain patterns of trait-based richness. In this example, a given group of organisms has 12 species, and a time-calibrated phylogeny among these species is shown. The pattern of trait-based richness here is that, for the character of interest, eight species have state A (blue) and four species have state B (green). The figure illustrates the three hypotheses that could explain the greater number of species with state A (i.e. the direct or proximate causes). Under the diversification rate hypothesis, there are more species with state A because species with state A have faster rates of diversification (speciation rate minus extinction rate) relative to state B, and so proliferate more rapidly. Under the trait origins hypothesis, state A is more common because it evolved more frequently (here, three different times, each indicated with a blue circle). Therefore, there can be more species with state A even though it originated more recently and does not increase diversification rates. Under the trait age hypothesis, state A is the ancestral state, and state B arose only recently within the group. Therefore, there has been too little time for species with state B to accumulate the same number of species as state A through speciation (and species with state B do not have high enough diversification rates to make up the difference). Note that this is merely a cartoon example intended to illustrate the three hypotheses with a limited number of species, and that there might be too few species to obtain significant results if these data were analysed statistically.

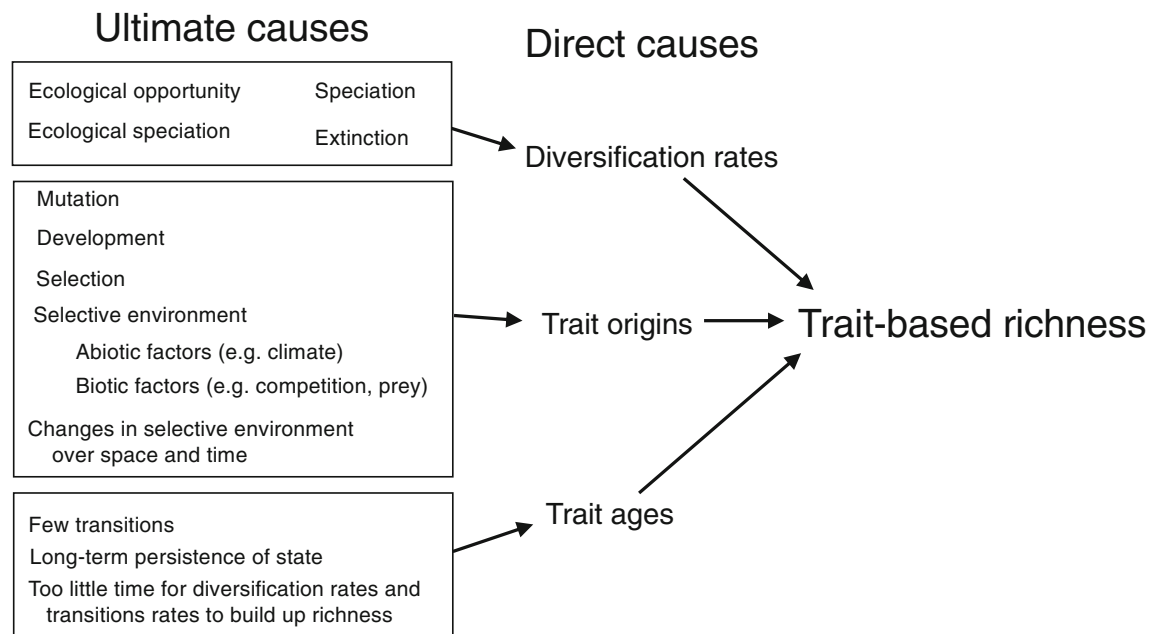


Fig. 4. The direct and ultimate causes of patterns in trait-based richness. Note that this is a comprehensive listing of the direct causes, but not a comprehensive listing of the ultimate causes.

determine the frequency of the state within populations. But large-scale patterns of trait evolution could also depend on the communities in which each species lives (e.g. whether local competitors already have this state) and large-scale biogeography (e.g. different community composition and abiotic conditions in different regions). Furthermore, these factors may differ depending on the hypothesis, the trait, and the group of organisms. Below I give a few examples of general principles that might apply.

If the diversification rate hypothesis is supported, then another level of explanation is to understand how and why the more species-rich state increases diversification rates. This could be because the state helps increase speciation rates, decreases extinction rates, or both. Certain states might promote speciation by promoting ecological divergence among populations and incipient species, which can foster **ecological speciation** (see Table 1; Nosil, 2012). For example, the presence of herbivory in some insects might help promote their speciation when different insect species specialise on feeding on different sets of plant species (e.g. Ehrlich & Raven, 1964; Hardy & Otto, 2014; Forbes *et al.*, 2017). Similarly, certain states might increase diversification by increasing **ecological opportunity** by allowing species with that state to use underutilised resources, and thereby reduce the potential constraints of competition on diversification (e.g. Schluter, 2000; Yoder *et al.*, 2010). More broadly, there is evidence that species interactions that have positive fitness effects for individuals of the focal clade can increase diversification rates (e.g. mutualism, parasitism for parasites), whereas those with negative fitness effects (e.g. competition, predation for prey) can decrease them (Zeng & Wiens, 2021b).

For the trait origins hypothesis, the evolutionary origins of a given state may depend on another variable. For example, the state might be most likely to evolve when species in a group disperse into a certain region or habitat in which that state is advantageous (e.g. if deciduousness evolves after invasion of temperate climates by woody angiosperms; Zanne *et al.*, 2014). Furthermore, a state might be more likely to evolve when the group disperses to a region where other species lack that state.

The simplest explanation underlying the trait age hypothesis is that there is a strong effect of incumbency, such that too little time has elapsed for an alternative state associated with higher diversification rates and/or transition rates to become as species rich as the ancestral state (see also online Supporting Information, Appendix S1, regarding ‘non-equilibrium hypotheses’). This incumbency effect may be even stronger if the differences in diversification and/or transition rates between states are limited (i.e. it will take much more time for small differences in these rates to lead to differences in richness). But many factors might also contribute, some of which intersect with the diversification rate and trait origins hypothesis. For example, the ancestral state may be maintained for lengthy periods of time with few transitions to an alternative state because of: (i) genetic constraints on the evolution of the alternative state; (ii) competition from co-

occurring lineages that already have that alternative state; and (iii) species that evolve the alternative state tend to go extinct, leaving little time for richness to build up among extant lineages having that state (e.g. Miller & Wiens, 2017).

There might also be ultimate explanations that span multiple hypotheses. For example, imagine a group of animals in which many species utilise an abundant dietary resource whereas a few species use a more limited one. The more limited resource might only be ‘colonised’ after the more abundant one was colonised (trait age hypothesis), and once it was fully utilised by a set of species, this might lower the subsequent diversification rates of species using this resource (diversification rate hypothesis), and also limit further transitions to this state from other states (i.e. trait origins hypothesis). However, these effects would need to be tested rather than simply being assumed. Furthermore, many trait-based richness patterns might not involve a limited resource at all, or at least not in the conventional sense (e.g. the paradox of sex).

Finally, some readers might ask: if these three hypotheses (diversification, trait origins, or trait age) are not the ultimate explanation for trait-based richness patterns, then why bother testing these proximate hypotheses at all? The answer is that the ultimate explanation may depend on which of these proximate hypotheses is supported. For example, it would be silly to test the ecological factors underlying differences in diversification rates as an explanation for richness patterns if those richness patterns were unrelated to variation in diversification rates. Thus, these three hypotheses are only a starting point for understanding the origins of trait-based richness patterns, but they are an essential starting point.

V. HOW DO WE INFER THE DIRECT CAUSES OF TRAIT-BASED RICHNESS PATTERNS?

How would one test among these three hypotheses (diversification rate, trait origins, trait age; Fig. 3)? Well-established macroevolutionary methods are available to test all three hypotheses. These methods generally require **time-calibrated phylogenies** for the group of interest. For example, **state-dependent speciation–extinction models** (SSE; Maddison, Midford & Otto, 2007; FitzJohn, 2012) offer a promising approach, and possibly the only one that can concurrently estimate **transition rates** between states, when each transition occurred, and the rates of speciation, extinction, and diversification associated with each state. The SSE approach has limitations (e.g. Maddison & FitzJohn, 2015; Rabosky & Goldberg, 2015), but potential solutions have also been developed. These solutions include models that incorporate the potential effects of other variables besides the trait of interest, specifically hidden state SSE, or HiSSE (Beaulieu & O’Meara, 2016; Nakov *et al.*, 2019). There are also many other approaches that can be used to estimate diversification rates. However, these methods generally estimate diversification rates for species or clades, not for states. These methods were

reviewed by Morlon (2014), and many new methods have been developed subsequently (e.g. Hoehna *et al.*, 2019; Maliet, Hartig & Morlon, 2019; Barido-Sottani, Vaughan & Stadler, 2020; Vasconcelos, O'Meara & Beaulieu, 2022). Many other methods can also be used to estimate **ancestral states** and transition rates across trees (e.g. Huelsenbeck, Nielsen & Bollback, 2003; Pagel, Meade & Barker, 2004; Beaulieu, O'Meara & Donoghue, 2013; Revell, 2014; Smaers, Mongle & Kandler, 2016; Pagel & Meade, 2022). None of these methods is perfect, but there is a large literature focused on testing the accuracy of these macroevolutionary methods in cases where the true answer is known, with simulations (e.g. Revell, 2014; Smaers *et al.*, 2016; Maliet *et al.*, 2019).

For brevity, I will focus here on SSE methods (although the same basic ideas should apply to other methods). SSE methods can be used to test all three hypotheses simultaneously and were designed to correct for the effects of different diversification rates (among states) on the estimation of transition rates and ancestral states (Maddison *et al.*, 2007). These effects may be problematic for methods that separately estimate diversification rates, transition rates, and ancestral states. However, SSE methods do require time-calibrated trees with dozens (if not hundreds) of species, relatively complete species sampling (preferably >50%), and no states should be too rare (present in <10% of sampled species). These requirements are addressed by FitzJohn, Maddison & Otto (2009) and Davis, Midford & Maddison (2013), among others. Importantly, the point here is not to review all relevant macroevolutionary methods, but rather to describe how these methods (in general) can be used to address the causes of trait-based richness patterns.

In the simplest case, the diversification rate hypothesis is supported when the state with the highest frequency among species has a significantly higher diversification rate than other states. The trait origins hypothesis is supported if there are significantly more transitions to the most frequent state than to other states (as inferred based on a higher estimated transition rate to this state). The trait age hypothesis is supported if the most frequent state is estimated to be the oldest state in the group (e.g. the state most likely to be present at the ancestral node; but see Appendix S2 for alternative approaches and discussion on the accuracy of ancestral-state reconstructions). The first two hypotheses can be readily tested by comparing the fit of the data to models based on the estimated diversification and transition rates relative to the fit of null models in which diversification rates and transition rates are equal between states. The diversification rate and transition rate (trait origin) hypotheses can be more strongly rejected by finding significant support for faster diversification rates and transition rates associated with the less common state, instead of the most common state. The trait age hypothesis can be tested by comparing the statistical support (e.g. proportional likelihoods) for reconstructing each of the alternative states at the root of the tree (see also Appendix S2). In the simplest cases, one hypothesis will be supported and the alternative hypotheses will be unsupported or rejected.

However, it is easy to imagine more complicated scenarios (see also Section VII). These three hypotheses are not mutually exclusive. If more than one hypothesis is supported, it may be difficult to tease apart the relative contributions of each hypothesis to determining the overall richness patterns among states. What makes this situation especially difficult is that the dependent variable (the species richness of each state), may have very few data points. For example, for a character with two states, there will be only two data points. This is an important methodological challenge for future studies. One potential solution is to use simulations based on the observed data (e.g. the tree and branch lengths), and evaluate how changing parameters (e.g. transition and diversification rates, ancestral states) influences the richness of each state relative to the observed data (following from O'Meara *et al.*, 2016). Estimating the relative contribution of different hypotheses to the observed richness patterns may be challenging overall. Fortunately, among the cases reviewed here, studies showing support for more than one hypothesis were actually in the minority (30%; see Section VI), and so this issue may not be problematic for most studies.

Recall that these three hypotheses are only an initial step in understanding the causes of trait-based richness patterns (see Section IV; Fig. 4). More research would be needed to link these results to the ultimate causes of these patterns. For example, if the diversification rate hypothesis is supported, then one can potentially estimate the contribution of speciation and extinction rates to the differences in diversification rates between states. Additional research could test the potential correlates and causes of increased speciation rates (or decreased extinction rates). Extinction rates may be estimated with much less precision than speciation rates for some methods (e.g. for HiSSE; Beaulieu & O'Meara, 2016). Yet, the ability of a method to estimate speciation and extinction rates should be evaluated with simulations on a method-by-method basis, not based on sweeping extrapolations from one or a few methods (e.g. Rabosky, 2010; Louca & Pennell, 2020). Furthermore, fluctuations in speciation and extinction rates within clades over time (the focus of Louca & Pennell, 2020) are not the focus here.

If the trait origins hypothesis is supported, then one can test for correlations between these evolutionary origins and other ecological and evolutionary variables. Many macroevolutionary methods have been developed to test for such correlations (e.g. Pagel, 1994; Huelsenbeck *et al.*, 2003; Ives & Garland, 2010; Adams & Collyer, 2018).

VI. WHAT IS KNOWN ABOUT THE CAUSES OF TRAIT-BASED RICHNESS PATTERNS?

Few studies have addressed the causes of trait-based richness patterns, especially in terms of these three hypotheses (Fig. 3). Nevertheless, I present here a brief, systematic review of the causes of trait-based richness patterns. I used information from 25 recent published studies. However, very few studies

were focused on explaining trait-based richness patterns and none focused on testing all three hypotheses.

To compile these studies, I searched for published analyses that used HiSSE (Beaulieu & O'Meara, 2016). These studies often estimated diversification rates associated with different states, different transition rates among states, and ancestral states at each node of the tree. Therefore, they potentially address all three direct hypotheses for trait-based richness patterns (Fig. 3). I focused specifically on studies that used HiSSE because this method is designed to address the potential impacts of hidden states and related criticisms of SSE methods (Beaulieu & O'Meara, 2016). Furthermore, as noted above, SSE methods were designed to correct for the effects of different diversification rates (among states) on the estimation of transition rates and ancestral states (Maddison *et al.*, 2007). Analyses that separately estimate diversification rates, transition rates, and ancestral states are potentially compromised by these effects.

I searched for studies that cited Beaulieu & O'Meara (2016) on *Google Scholar* on 17 December 2021. I sorted studies by relevance and examined the first 150 papers. I only included studies that contained: (i) information on the species richness of the different states (directly or indirectly); (ii) ancestral reconstructions of states; and (iii) a comparison of diversification rates between states. Information on estimated transition rates among states was somewhat patchy among studies, and so is addressed separately below. Again, very few studies were actually focused on testing hypotheses about trait-based richness.

I found 25 papers that met these criteria. Five of these papers included two usable characters each, yielding a total of 30 data points (Table 2). Among these 30 data points, 13 were from animals, 2 from protists, and 15 from plants. Various characters were analysed, including diet and habitat in animals and growth form and reproductive systems in plants. I assigned data points to each hypothesis as described in the preceding section.

The results of these case studies most frequently supported the trait age hypothesis over the diversification rate hypothesis, by almost two to one (Fig. 5). Thus, in these 15 cases that supported the trait age hypothesis, the most species-rich state among species was the one that evolved earliest in the tree (trait age hypothesis), not the state associated with higher diversification rates (diversification rate hypothesis). Indeed, the majority of these 15 cases showed significant differences in diversification rates among states ($n = 9$), but with higher diversification rates associated with the less common state. This latter result strongly rejects the diversification rate hypothesis in these case studies (i.e. under the diversification rate hypothesis, there should be significantly faster diversification rates in the most common character state, not the less common state). The diversification rate hypothesis was supported exclusively in eight cases. A minority of cases supported both ($n = 4$) or neither ($n = 3$).

These results were broadly similar between animals and plants. For example, the trait age hypothesis was supported in 10 of 13 cases in animals (77%) and in 9 of 15 cases in

plants (60%). The diversification rate hypothesis was supported exclusively in two out of 13 cases in animals (15%) and three out of 15 cases in plants (20%). The support for each hypothesis did not seem to be an artifact of the age of the group analysed or the number of species sampled in that group (see Table 2 legend).

Not all studies reported transition rates among states. Nevertheless, 20 data points had this information. Only six of these cases (30%) supported the transition rate hypothesis, by showing that the highest estimated transition rate was to the most common state. Among these studies, three also supported the diversification rate hypothesis (but not the trait age hypothesis), whereas three also supported the trait age hypothesis (but not the diversification rate hypothesis). In short, relatively few studies supported the transition rate hypothesis, and none did so to the exclusion of the other two hypotheses. Almost all cases in which two or more hypotheses were supported were in plants (8/15 cases compared to 0/13 in animals).

Many studies were motivated by the idea that the trait of interest might influence diversification rates. Therefore, the sampling of studies here was potentially biased to favour the diversification rate hypothesis. Yet, the diversification rate hypothesis was supported exclusively only about half as often as the trait age hypothesis (Fig. 5).

Clearly, this survey will not be the final word on the causes of trait-based richness patterns. Nevertheless, there are tantalising findings. There is support for all three hypotheses, but with more studies supporting the trait age than the diversification rate hypothesis (and with even less support for the trait origins hypothesis). This result is important for two reasons. First, almost none of the original studies focused on testing the trait age hypothesis. Therefore, it is crucial for future studies to consider the trait age hypothesis, and not merely the diversification rate hypothesis. At the same time, failing to support the diversification rate hypothesis does not guarantee that the trait age hypothesis will be supported instead (e.g. there were three cases in which neither hypothesis was supported; Fig. 5). Second, the widespread importance of time (trait age) for explaining trait-based richness has clear parallels to recent analyses of spatial richness, in which colonisation time also seems to be the most broadly important explanation for richness patterns across clades, based on broad-scale reviews (Jansson *et al.*, 2013; Li & Wiens, 2019). These results hint that there may be similar general causes for diverse types of species richness patterns (in the majority of cases). I address this further in Section IX.3.

VII. ADDING COMPLEXITY

So far, I have focused primarily on the simplest pattern of trait-based richness: the total number of species having each state of a discrete character among all species within a single group of organisms (Fig. 1A). There are at least four types of more complex trait-based richness patterns (Fig. 1B–E). First,

Table 2. Case studies of the causes of trait-based richness patterns.

Group	Trait	Trait frequencies	Anc. state	Div. rate	Tran. rate	Clade age (Myr)	Species sampled	Source
Animals	Diet	Carnivory: 59–64% Omnivory: 1–2% Herbivory: 35–39%	Yes	No	—	800	1087	Román-Palacios <i>et al.</i> (2019)
Insects (Orthoptera)	Acoustic communication	Present: 39% Absent: 61%	Yes	No	No	350	249	Song <i>et al.</i> (2020)
Bees (Tapinotaspidini)	Habitat	Open: 65% Forest: 35%	Yes	No*	—	60	52	Aguiar <i>et al.</i> (2020)
Bees (Tapinotaspidini)	Oil collection	Malpighiaceae: 56% Malpig. + other: 17% Non-Malpig.: 27%	Yes	No	—	60	52	Aguiar <i>et al.</i> (2020)
Acorn ants	Nesting site	Arboreal: 37% Terrestrial: 63%	Yes	No	No	55	103	Prebus (2017)
Acorn ants	Social parasitism	Free-living: 92% Parasitic: 8%	Yes	No	No	55	103	Prebus (2017)
Insects (weevils)	Host plant	Brassicaceae: 34% Non-Brassicaceae: 66%	Yes	No*	No	80	204	Letsch <i>et al.</i> (2018)
Pholcid spiders	Microhabitat	Ground: 37% Leaf: 31% Space: 32%	Yes	No*	—	—	600	Eberle <i>et al.</i> (2018)
Tetrapods (vertebrates)	Diel activity	Diurnal: 51% Nocturnal: 41% Arrhythmic: 6% Crepuscular: 1%	No	Yes*	—	350	1914	Anderson & Wiens (2017)
Tetrapods (vertebrates)	Acoustic communication	Present: 69% Absent: 31%	No	No	—	350	1799	Chen & Wiens (2020)
Snakes	Habitat	Arboreal: 17% Non-arboreal: 83%	Yes	No	—	128	1252	Harrington <i>et al.</i> (2018)
Snakes	Habitat	Fossorial: 15–18% Non-fossorial: 82–85%	No	Yes*	No	128	1256	Cyriac & Kodandaramaiah (2018)
Hyperoliid frogs	Dichromatism	Dichromatic: 34% Monochromatic: 66%	Yes	No*	No	—	173	Portik <i>et al.</i> (2019)
Diatoms	Habitat	Freshwater: 70% Marine: 30%	No	Yes*	Yes	200	1132	Nakov <i>et al.</i> (2019)
Diatoms	Habitat	Benthic: 70% Planktonic: 30%	No	Yes*	—	200	1132	Nakov <i>et al.</i> (2019)
Plants (liverworts)	Sexual systems	Bisexual: 28% Unisexual: 72%	Yes	No*	Yes	—	297	Laenen <i>et al.</i> (2016)
Plants (monocots)	Growth form	Geophytes: 48% Non-geophytes: 52%	No	No*	No	—	12779	Howard <i>et al.</i> (2020)
Plants (Amaranthaceae)	Flower	Sterile: 38% Not sterile: 62%	Yes	Yes*	No	55	63	Di Vincenzo <i>et al.</i> (2018)
Plants (Annonaceae)	Habit	Tree/shrub: 77% Liana: 23%	Yes	No*	No	90	835	Xue <i>et al.</i> (2020)
Plants (Annonaceae)	Pollen dispersal	Solitary: 71% Compound: 29%	Yes	Yes*	No	90	835	Xue <i>et al.</i> (2020)
Plants (Cynoglossoidae)	Dispersal	Glochid: 60% Absent: 40%	Yes	Yes*	No	50	192	Otero <i>et al.</i> (2020)
Plants (Gesneriaceae)	Pollination	Hummingbird: 70% Non-hummingbird: 30%	No	Yes*	No	60	583	Serrano-Serrano <i>et al.</i> (2017)
Plants (Lamiaceae)	Sexual system	Gynodioecious: 11% Non-gynodioecious: 89%	Yes	No*	—	—	536	Rivkin <i>et al.</i> (2016)
Plants (Melastomataceae)	Dispersal mode	Abiotic: 42% Biotic: 58%	No	Yes	Yes	75	1684	Reginato <i>et al.</i> (2020)

(Continues on next page)

Table 2. (Cont.)

Group	Trait	Trait frequencies	Anc. state	Div. rate	Tran. rate	Clade age (Myr)	Species sampled	Source
Plants (Onagraceae)	Mating system	Self-compatible: 79% Self-incompatible: 21%	No	No*	Yes	100	292	Freyman & Hohna (2019)
Plants (<i>Penstemon</i>)	Pollination	Hummingbird: 18% Non-hummingbird: 82%	Yes	Yes*	No	—	120	Wessinger <i>et al.</i> (2019)
Plants (Plantiganaceae)	Nectar spurs	With spurs: 70–80% Without: 20–30%	No	Yes*	Yes	50	296	Fernandez-Mazuecos <i>et al.</i> (2019)
Plants (Polemoniaceae)	Flower colour	Non-pigmented: 24% Anthocyanin: 69% Carotenoid: 4% Chlorophyll: 2%	No	Yes*	No	92	429	Landis <i>et al.</i> (2018)
Plants (Polemoniaceae)	Pollination	Autogamous: 33% Outcrossing: 67%	Yes	No	Yes	92	492	Landis <i>et al.</i> (2018)
Plants (Rubiaceae)	Growth form	Woody: 34% Herbaceous: 66%	Yes	No*	No	90	103	Neupane <i>et al.</i> (2017)

For each study, the study group, trait analysed, and estimated trait frequencies are given, along with the estimated age of the clade and the number of species sampled in the tree.

'Anc. state' indicates whether the most common state in the group is the most likely estimated ancestral state (Yes *versus* No).

'Div. rate' indicates whether or not the most frequent state in the group has the highest estimated net diversification rate (with Yes indicating that it does, and No indicating no difference in rates or higher rates in a less common state). Studies in which the differences in rates between traits are significantly different are identified with an asterisk (No and an asterisk indicates that the less common state is associated with significantly higher diversification rates).

'Tran. rate' indicates whether or not the highest transition rate (or estimated number of transitions) consists of transitions to the most common state in the group. Many studies did not clearly present these transition rates (indicated with —).

The clade age is the crown-group age of the ingroup for the case study. Note that in many cases, the ages of clades are approximate since they were not stated by the authors and so were estimated from the figures. Furthermore, several studies ($n = 6$) did not present this information in the text or figures, and so these studies were not included in the statistical comparisons (—).

Species sampling is the number of species in the tree used by the authors in their macroevolutionary analyses.

Unpaired *t*-tests (in R) were used to test whether support for the diversification rate hypothesis and trait age hypothesis was related to the ages of clades or species sampling in each study. These tests found no significant difference in clade ages ($P = 0.4128$) between studies that supported the diversification rate hypothesis (mean = 122.7 million years, Myr) and those that did not (mean = 177.7 Myr). Similarly, there was no significant difference in species sampling ($P = 0.6165$) between studies that supported the diversification rate hypothesis (mean = 803 species sampled) and those that did not (mean = 1167 species). There was also no significant difference in clade ages ($P = 0.8346$) between studies supporting the trait age hypothesis and those that did not (mean supporting = 146.8 Myr; mean not supporting = 160.5 Myr) nor was there a significant difference ($P = 0.1411$) in species sampling (mean supporting = 387 species; mean not supporting = 2118 species).

Studies are listed taxonomically, starting with animals, then protists, and then plants.

there can be spatial variation (Fig. 1B) in trait-based richness patterns (e.g. a higher proportion of species with state A in tropical regions relative to temperate regions). Such patterns have been documented in many cases (e.g. Bennie *et al.*, 2014; Moeller *et al.*, 2017). The causes of these spatial trait-based patterns can be complex (because of the addition of dispersal), and I briefly describe and illustrate these causes in Fig. 6. Second, trait-based richness patterns can vary among clades (Fig. 1C). Thus, a given state may occur at a higher frequency among species in one clade than another, or these patterns might vary across multiple clades (see example later in this section, Fig. 7 and Table S1). Third, there can be richness patterns in continuous variables (e.g. body size) rather than in simple discrete traits (Fig. 1D). Fourth, we can consider trait-based richness in multiple characters simultaneously (Fig. 1E). For example, there might be certain combinations of states among characters that are particularly common or rare (e.g. most species in a group have state A of character 1 and state B of character 2, whereas far fewer species have the combinations A:A, B:B, or B:A). There can also

be combinations of all four types (e.g. spatial variation among clades in multiple continuous characters). The species richness of parasites (or other associates) on a host species might be considered yet another type of trait-based richness (see Appendix S3).

Despite this complexity, the same basic principles outlined above should generally apply. That is, trait-based richness patterns should depend on diversification rates, trait origins, and trait ages (Fig. 3). Thus, the same three hypotheses should apply when comparing different clades, when analysing a continuous variable, and when analysing combinations of two or more traits. However, dispersal may also influence spatial trait-based patterns, which greatly increases the number of possible explanations for these spatial patterns (Fig. 6). Furthermore, interactions among traits and their states may be important when considering multiple traits, or even single traits. For example, it may be that only certain combinations of states among different traits can increase diversification (e.g. O'Meara *et al.*, 2016). But these interactions will influence species richness through their impacts on diversification,

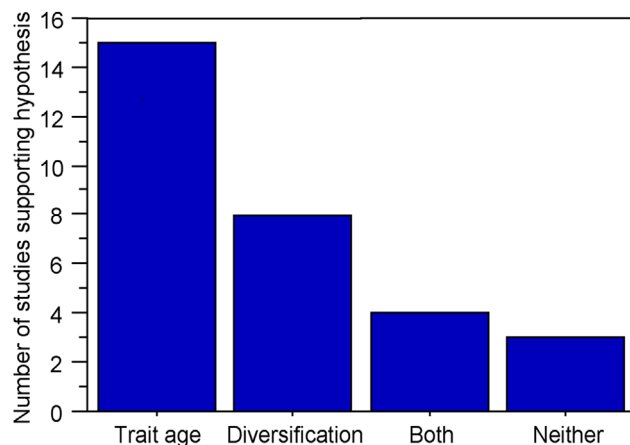


Fig. 5. The causes of trait-based richness patterns from a survey of case studies. A total of 25 case studies were used, five of which included two traits each (total of 30 cases). In all 30 cases, a given state of one trait was more frequent among species in the clade than the other state (Table 2). Only studies that tested both the trait age and diversification rate hypotheses were included here. In 15 cases, the trait age hypothesis was supported (i.e. the oldest state is the more common state) and the diversification rate hypothesis (i.e. faster rate in the more common state) was not. For eight cases, only the diversification rate hypothesis was supported. In the remaining seven cases, either both hypotheses were supported (four cases) or neither were (three cases).

transition rates, and the amount of time in each state (or combination of states). Of course, it will be difficult to distinguish the effects of traits that are perfectly correlated in their distribution among species.

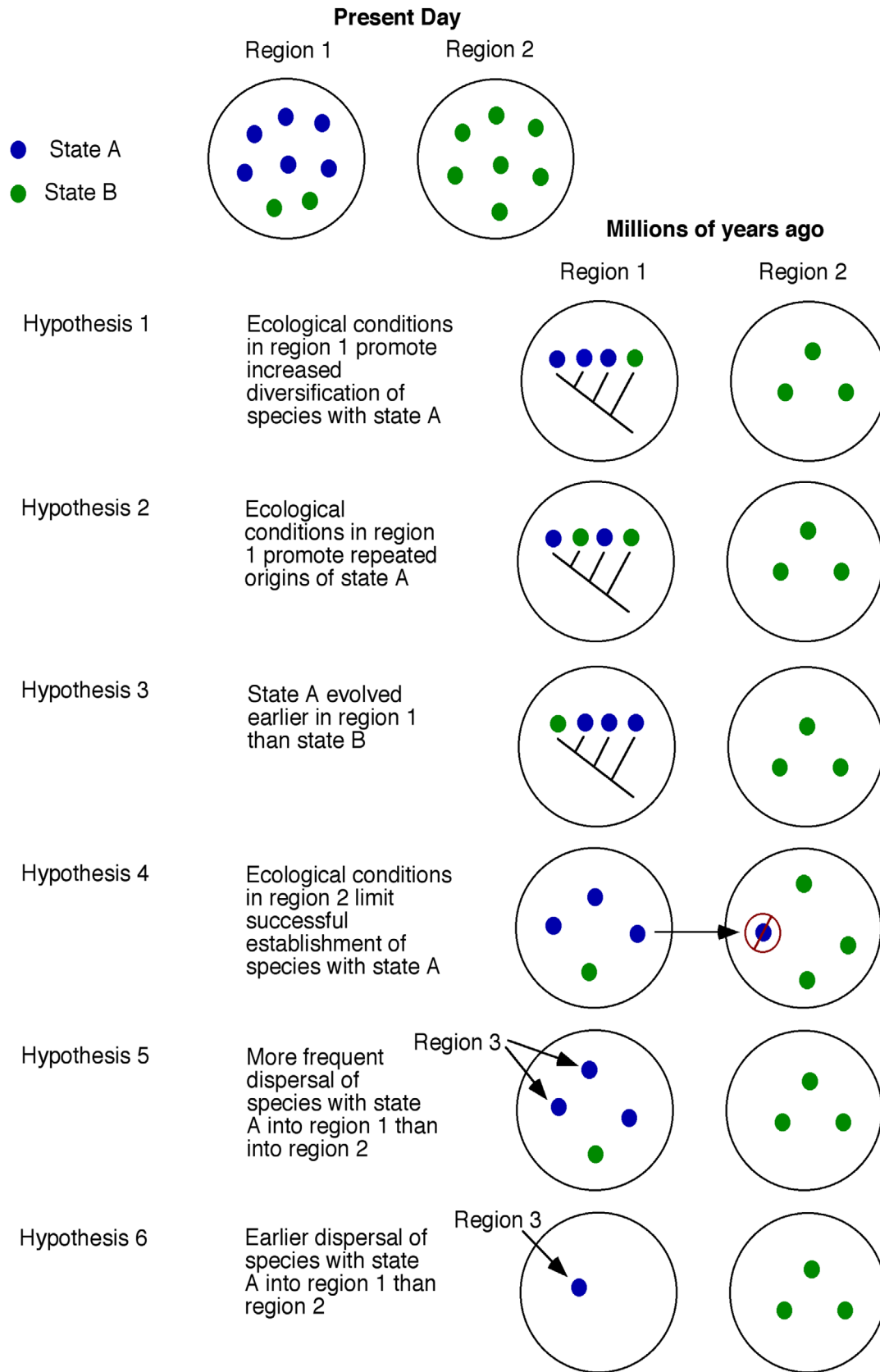
Many of these more complex scenarios can be analysed with existing methods. First, there are well-established model-based methods for estimating patterns of dispersal among species and regions (e.g. Ree & Smith, 2008; Landis *et al.*, 2013). These can be used to help understand how dispersal contributes to the origins of spatial trait-based richness patterns. Second, the methods used for analysing patterns within each clade can be applied to multiple clades to evaluate how differences in trait-based richness patterns arise among clades (see example below in this section). Third, SSE methods are available for estimating diversification rates associated with continuous characters (QuaSSE; FitzJohn, 2010), and methods are available for estimating ancestral values of continuous traits (e.g. Smaers *et al.*, 2016). Furthermore, although analysing species richness for continuous variables may require binning them into a finite number of categories, different choices about the definition and number of bins need not impact the overall conclusions (e.g. see Appendix S3 in Hutter, Guayasamin & Wiens, 2013). Fourth, although analysing multiple traits may be more challenging, this has been done previously. O'Meara *et al.* (2016) examined the factors that determined the number of species with each combination of states for six floral traits. They used multi-state SSE methods (MuSSE) to estimate rates for different combinations of states

across traits, and used simulations to test if these rates could explain the observed patterns of trait-based richness. In summary, the point here is that addressing these more complex scenarios of trait-based richness is not necessarily out of reach for existing methods. Nevertheless, analysing these complex scenarios might benefit from the development of new methods, or novel combinations of existing methods.

Case studies of the direct causes of these more complex trait-based richness patterns are rare. Nevertheless, a recent analysis of the evolution of reproductive modes in amphibians (Liedtke, Wiens & Gomez-Mestre, 2022) can be used to compare the causes of trait-based richness patterns among clades. There are three major groups of living amphibians (Fig. 7): frogs (Anura), salamanders (Caudata), and caecilians (Gymnophiona; worm-like, legless, tropical, burrowing amphibians). Their trait-based richness patterns in reproductive modes are shown in Fig. 7 and Table S1. Although many of the same reproductive modes are present in all three groups (e.g. direct development), the most species-rich mode is different in each group. In frogs and caecilians, the most species-rich mode (aquatic and semi-terrestrial, respectively) is also the ancestral mode, supporting the trait age hypothesis. There is no significant association between reproductive modes and diversification rates in frogs or caecilians. In salamanders, the most species-rich reproductive mode (direct development) is associated with significantly higher diversification rates, and is not the ancestral state, clearly supporting the diversification rate hypothesis. Intriguingly, in all three groups, the fastest estimated transition rates are to modes with limited richness (Fig. 7). In salamanders, the frequent transitions to paedomorphosis (no adult stage) are counterbalanced by negative estimated diversification rates (extinction exceeds speciation), which help keep this mode relatively rare. In summary, differences in trait-based richness among these three clades are explained by the trait age hypothesis and different ancestral states in two clades (in frogs and caecilians) and a novel relationship between diversification and one of these states in a third clade (salamanders). As frequently found in the review of within-clade patterns, transition rates are generally decoupled from richness patterns across clades.

VIII. THE PROBLEM OF IGNORING TRAIT-BASED RICHNESS

Trait-based richness patterns are not a major focus in most ecological or evolutionary studies, but ignoring them might nevertheless be problematic in some cases. As one example, many studies on spatial richness patterns in plants focus on woody angiosperms, including studies that analysed the macroevolutionary causes of these patterns (e.g. Kerkhoff, Moriarity & Weiser, 2014; Qian *et al.*, 2015; Craven *et al.*, 2019; Segovia *et al.*, 2020). These studies often implicitly assume that the main drivers of richness patterns are the speciation, extinction, and dispersal of these woody plant



(Figure 6 legend continues on next page.)

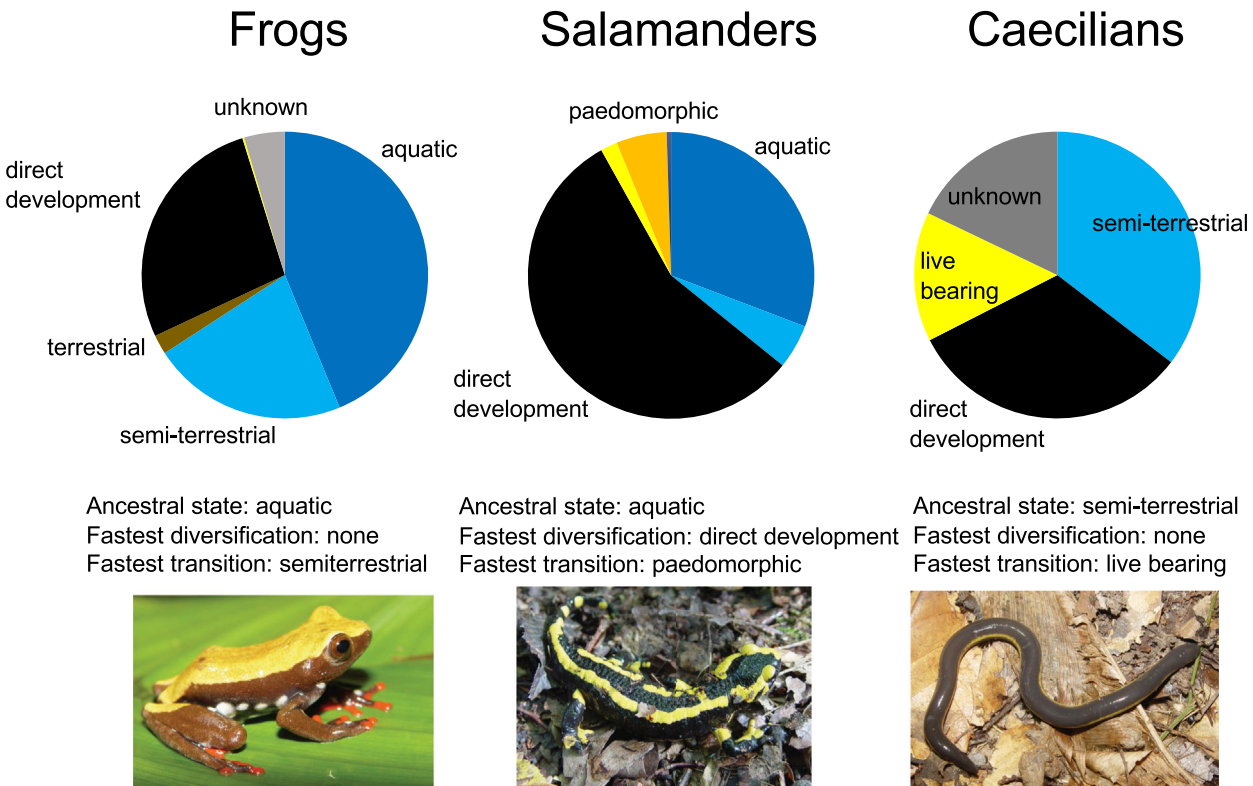


Fig. 7. Comparing the origins of trait-based richness patterns among clades: amphibian reproductive modes. Liedtke *et al.* (2022) estimated the number of species with each reproductive mode in anurans (frogs; 7097 species), caudates (salamanders; 738 species), and caecilians (212 species). Most described species were included in each clade (>94%). The pie diagrams show the percentage of species with each mode in each clade, based on the sampled species (numbers given in Table S1). Liedtke *et al.* (2022) also estimated diversification rates associated with each mode, the ancestral modes at the root of the tree for each clade, and transition rates among modes. In frogs and caecilians, the most species-rich state is the ancestral state (aquatic and semi-terrestrial, respectively), supporting the trait age hypothesis. Reproductive modes and diversification rates are decoupled in these two groups. In salamanders, the most species-rich state (direct development) has a significantly higher diversification rate, and is not the ancestral state (which is aquatic). In all three groups, the fastest transition rates are to modes that are relatively species-poor, including semi-terrestrial (frogs), paedomorphosis (salamanders), and live-bearing (caecilians). Modes are defined as follows: aquatic (eggs laid in water, aquatic larvae), semi-terrestrial (eggs laid out of water, aquatic larvae), terrestrial (eggs and larvae both out of water), direct development (terrestrial eggs, no larvae), live bearing (no external eggs or larvae), paedomorphic (adults reproduce as aquatic larvae). The three species shown are (left to right): Bolifamba reed frog (*Hyperolius bolifambae*); fire salamander (*Salamandra salamandra*); Banna caecilian (*Ichthyophis bannanicus*). All photographs by J. J. Wiens.

(Figure legend continued from previous page.)

Fig. 6. The causes of spatial patterns of trait-based species richness. In this simplified example, two regions are presently inhabited by a clade (top). Region 1 presently has eight species, 75% with state A (blue) and 25% with state B (green). Region 2 presently has seven species, all with state B. Six non-exclusive hypotheses could help explain this spatial variation in trait-based richness. These are illustrated by showing richness patterns several million years ago. Assuming that state B is the ancestral state for the clade, there might be a higher frequency of state A in region 1 because state A increased diversification rates in region 1 (hypothesis 1: regional diversification), because state A evolved more frequently in region 1 (hypothesis 2: regional origins), or because state A evolved earlier in region 1, and state B evolved only recently (hypothesis 3; regional age). Hypotheses 1–3 assume little dispersal between regions, and are similar to the diversification rate, trait origins, and trait age hypotheses within a single clade (but assuming that ecological conditions in one region promote diversification or repeated origins of one of the states). Hypotheses 4–6 incorporate dispersal (or lack thereof). Under hypothesis 4 (limited dispersal), the disparity in trait-based richness between regions is maintained by failure of species with state A to establish in region 2 (this could also maintain differences in richness of states between regions that were generated by hypotheses 1–3). Hypotheses 5 and 6 assume that species of this clade occur in other regions besides regions 1 and 2 (i.e. region 3). Under hypothesis 5 (repeated dispersal), there are more species with state A in region 1 because there is repeated dispersal of species with state A into region 1 (but not region 2) from another region (region 3). Under hypothesis 6 (ancient dispersal), there is ancient dispersal of state A into region 1 (from region 3) and more recent dispersal of state B into region 1 from region 2 (not shown), such that state A eventually outnumbers state B in region 1.

lineages (e.g. the relative timing of dispersal to different areas was a focus of many of the studies cited above). But these are actually studies in trait-based richness: woody plants are defined based on a shared character state. Importantly, richness patterns in woody plants may be influenced by the rate and timing of transitions between the woody and non-woody states (Fig. 6), variables that were not included in these studies. For example, high richness of woody plants in a region might be related to more frequent transitions from the non-woody to woody state there, or earlier transitions from the non-woody to woody state (and not earlier dispersal from other regions). Indeed, the causes of spatial richness patterns in trait space can be quite complicated (Fig. 6). In short, by considering the origins of trait-based richness patterns, we can see that the causes of spatial richness patterns that were inferred by looking only at species with one character state may be mistaken (or at least far more complex). Future studies should recognise the limitations of this study design and avoid it, regardless of whether one can prove that these past studies were strongly misled.

IX. UNANSWERED QUESTIONS

In this section, I discuss several unanswered questions about trait-based richness patterns. I start with questions raised by the systematic review herein (Fig. 5), and then move on to more general questions.

(1) Are diversification rates overrated?

The systematic review here suggests that trait-based richness patterns are often not explained by variation in diversification rates among states (Fig. 5). Indeed, in many cases, diversification rates were significantly higher in the less common state. This finding parallels many studies of spatial richness patterns that often show faster diversification rates in locations with fewer species, such as temperate regions (e.g. Jetz *et al.*, 2012; Rabosky *et al.*, 2018; Igea & Tazentzap, 2020). Yet, diversification rates are often the primary focus of analyses of spatial and trait-based richness patterns, to the exclusion of other hypotheses (e.g. as in the three studies cited above).

Why do diversification rates often fail to explain these trait-based and spatial richness patterns? Simulations of spatial richness patterns may offer some insights (Pontarp & Wiens, 2017). These simulations show that even when ecological conditions favoured faster diversification rates (e.g. in some habitats), those faster diversification rates did not translate into higher species richness until after considerable time had elapsed. Until that point in time, richness patterns tended to be dominated by incumbency (i.e. whichever habitat was successfully colonised first had the highest richness).

Given this idea, one interpretation of the empirical patterns is that the importance of time in many analyses

of spatial and trait-based richness reflects the limited scope of many studies (e.g. if they focused on larger groups and/or older timescales, they might find that diversification rates explained richness patterns instead; see also Schluter, 2016). However, this does not necessarily make the conclusions of smaller-scale analyses incorrect for the group and timescale examined. Furthermore, the analyses here showed no significant effect of a clade's size or age on whether there was support for the diversification rate or the trait age hypothesis (Table 2), despite a range of clade ages from 50 to ~800 million years. Along with more empirical studies of the causes of trait-based richness patterns, theoretical studies should also be invaluable in understanding the differences in results among empirical studies.

(2) Why are transition rates not transformative?

The systematic review here (Table 2) found no cases in which variation in transition rates among states (trait origins hypothesis) was the sole explanation for trait-based richness patterns. Furthermore, in most cases in which transition rates were estimated (70%), these studies found higher transition rates to the less common state (the opposite of the pattern expected if transition rates explained which state was most common). Why do transition rates seem to be so irrelevant?

There may be several contributing factors. Each new origin of a state will (by itself) generate only a single descendent species with that state. Therefore, transition rates might be most important for generating higher richness if these origins are relatively ancient in the tree and/or associated with faster diversification rates. Indeed, a single origin of a state may be sufficient for that state to become almost universal within a group (e.g. viviparity among living mammals). Furthermore, as a state becomes more common within a group over its evolutionary history, the number of additional transitions to that state may decrease (e.g. there will be proportionally fewer species from which these new transitions can arise). Thus, we might expect more transitions to the less common state overall, and that is consistent with the patterns observed most frequently here (Table 2). However, these ideas should be tested explicitly with simulations.

The relative unimportance of transition rates for explaining trait-based richness patterns has intriguing parallels with dispersal rates for spatial richness patterns. For example, an analysis of 15 groups of animals and plants found no cases in which regional richness patterns were explained primarily by variation in the frequency of dispersal among regions (Li & Wiens, 2019). Instead, these spatial richness patterns were generally explained by the timing of colonisation of different regions (i.e. higher richness in regions that were colonised earlier).

(3) Are there generalities underlying all three types of richness patterns?

Comparison of the findings of the systematic review here (Fig. 5) with similar analyses of regional richness patterns

(Li & Wiens, 2019) suggests that there may be broad generalities in the causes of spatial and trait-based richness patterns across many plant and animal clades. In short, based on these case studies, the timing of transitions between states (trait-based) and locations (spatial) seems to be the most generally important factor explaining these richness patterns, whereas diversification rates are generally less important, and the number of transitions even less so. Confirming (or refuting) these generalities should be a ripe area for future research.

What about clade-based richness? Analyses across living organisms have suggested that clade-based richness patterns are generally explained by diversification rates and not by clade ages (Scholl & Wiens, 2016). However, these analyses compared only taxa of the same rank (e.g. families to families, phyla to phyla), and taxa of the same rank may be more similar in age than a random selection of clades. By contrast, dispersal and character-state transitions can occur anywhere in a tree. Therefore, clade ages might be more important for explaining clade-based richness if clades of any age were compared (Wiens, 2017). Resolving this question could help determine if there are generalities that span all three types of species richness.

(4) What are the most important ‘ultimate’ causes of trait-based richness patterns?

At present, there are very few studies that have tested the proximate explanations for trait-based richness patterns (i.e. the diversification rate, trait origins, and trait age hypotheses). Even fewer studies (if any) that have linked these richness patterns to their proximate causes have then tied those proximate causes to their ultimate causes. Finding generalities in these ultimate causes should be an important long-term goal for future studies of trait-based richness. For example, are ultimate causes that are related to competition for limited resources and release from that competition (e.g. ecological opportunity) generally the most important? Or is simple incumbency in state origins more broadly important instead? What about within-species processes that impact speciation and trait evolution?

(5) Do communities, regions, or clades ‘fill up’ with species having similar traits?

A major question in ecology and evolution is whether clades, regions, and local communities become saturated (i.e. filled up) with species over time, such that no new species can be added unless a species that is already present goes extinct (e.g. Elton, 1950; MacArthur & Wilson, 1963; Terborgh & Faaborg, 1980; Tilman, 2011). Strangely, much of the recent literature that is based on this idea tends to ignore species’ traits, especially studies focused on clades and regions. But why would a clade or region fill up with species unless those species were competing for a shared, limited resource? Clearly, this will depend on their traits, particularly those relevant to potentially limited resources (e.g. diet,

microhabitat). Analyses of trait-based richness patterns offer several potential avenues to address this topic.

For example, one approach is to analyse patterns of trait-based richness among local communities and among regions, combined with estimates of trait evolution and biogeographic dispersal among regions. With these data and tools, one can ask: is the local richness of species that share the same state related to the time that the state has been present in the region (either through *in-situ* evolution of the trait or dispersal of the trait from other regions)? For example, is there a positive, linear relationship between the local richness of species with that state in each region and when the state originated in each region? Or does local richness of those species instead seem to plateau over time among regions, suggesting saturation of species with that state (or combination of states) in local communities over time? If lineages having that state are added to some communities through dispersal from other regions, do those communities have increased local richness of species with that state relative to other communities? Or is local richness of species with that state similar across all these communities, suggesting that there is a limit on how many species with that state a local community can support? This is just one possible approach (among many) for applying trait-based richness to look for signals of community saturation. Along these lines, an important caveat is that the relationship between trait differences among species and their co-existence is not necessarily straightforward and may involve multiple traits with different effects (e.g. Kraft, Godoy & Levine, 2015).

(6) Do parallel adaptive radiations in different locations generate parallel patterns of trait-based richness?

In recent decades there has been burgeoning interest in adaptive radiation (Schluter, 2000; Glor, 2010; Gillespie *et al.*, 2020), and especially replicate adaptive radiations in sets of nearby locations. These locations include African rift lakes for cichlids (Seehausen, 2006), Greater Antillean islands for *Anolis* lizards (Losos *et al.*, 1998), and isolated Neotropical cloud forests for *Viburnum* shrubs (Donoghue *et al.*, 2022). These replicate radiations often generate similar sets of ecomorphs in each location (i.e. species with characteristic ecologies and associated morphologies). However, few studies (if any) have explored whether parallel adaptive radiations generate parallel patterns of trait-based richness. For example, does the same ecomorph become the most species rich in each of the parallel radiations? Or do different ecomorphs dominate in each one? If the latter pattern is supported, is this related to different orders in which ecomorphs evolved in each parallel radiation? Or might similar richness patterns develop in each radiation, even when the oldest ecomorph in each radiation differs? If so, might this be related to certain ecomorphs having consistently faster diversification rates than other ecomorphs in each radiation?

To give a simple example along these lines (Fig. 8), previous research has shown that there are several

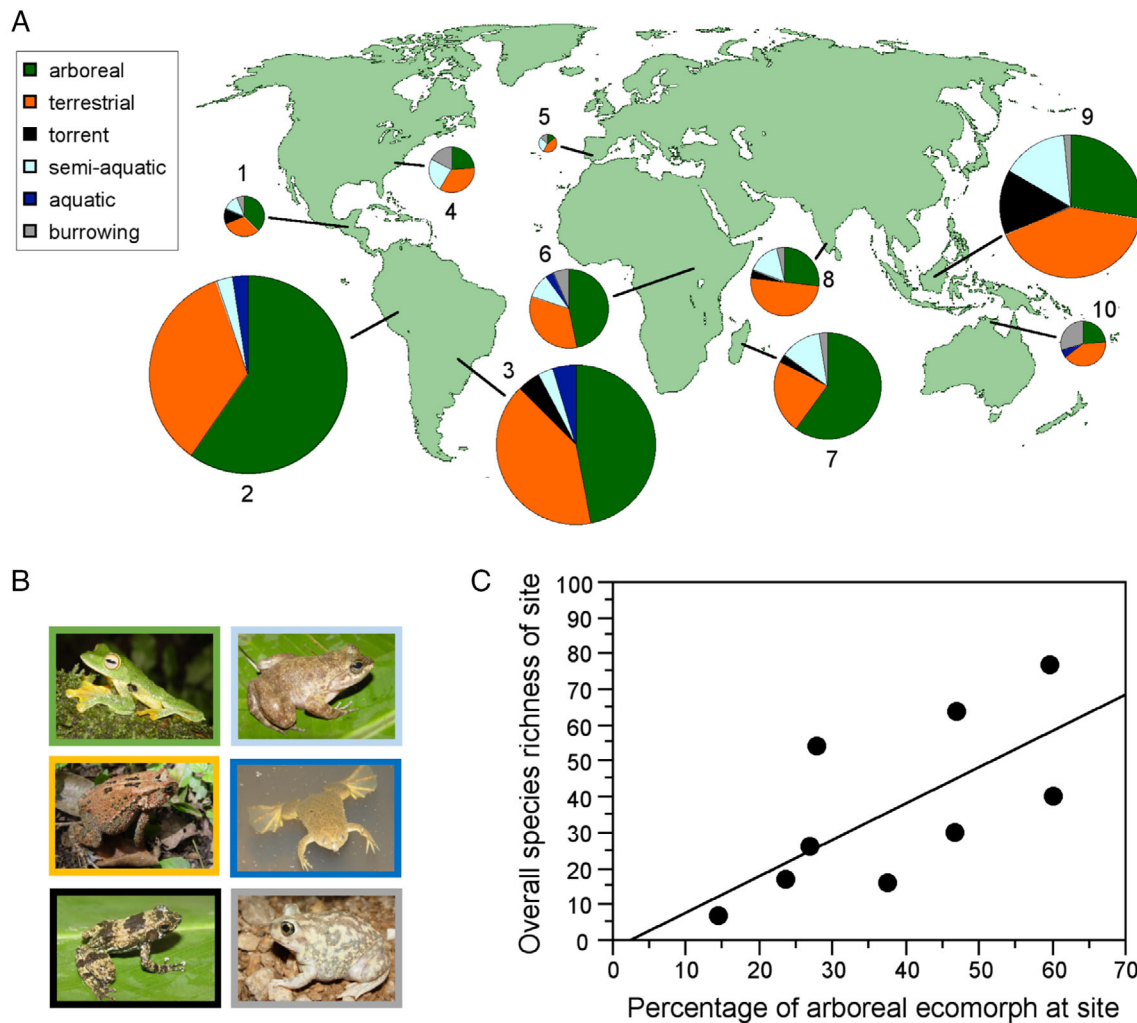


Fig. 8. Patterns of trait-based (ecomorph) richness and overall species richness in frogs. (A) 10 sites having data on overall species richness (size of pie chart) and proportional richness of ecomorphs (trait-based richness). Note that not all ecomorphs are present at every site. Details on the 10 sites are provided in Table S2 and in Moen *et al.* (2016). The 10 sites are in: 1, Guatemala; 2, Peru; 3, Brasil; 4, USA; 5, Spain; 6, Uganda; 7, Madagascar; 8, India; 9, Borneo; 10, Australia. (B) A representative of each of the six ecomorphs. The colours around each image correspond to ecomorph colors in A. (C) Significant, positive correlation between the percentage of the arboreal ecomorph at each site and the overall species richness of frogs at that site ($\rho = 0.756$; $P = 0.011$). The six species shown in B are: arboreal = *Rhacophorus reinwardtii*; terrestrial = *Sclerophrys maculata*; torrent-dwelling = *Mantidactylus lugubris*; semi-aquatic = *Mantidactylus grandidieri*; aquatic = *Xenopus victorinus*; burrowing = *Scaphiopus couchii*. All photographs by J. J. Wiens.

distinct ecomorphs of frogs, with morphologies that are strongly related to their different adult microhabitats (e.g. Moen, Morlon & Wiens, 2016). These include aquatic, semi-aquatic, arboreal, burrowing, terrestrial, and torrent ecomorphs (the latter occur in fast-flowing streams). The species richness of different ecomorphs was previously estimated for 10 globally distributed sites (Fig. 8), as was the ancestral ecomorph for major frog clades and families (Moen *et al.*, 2016). The terrestrial ecomorph was ancestral for most major clades, and is the numerically dominant ecomorph at many sites (Fig. 8), including those in Asia (Borneo, India), Australia, Central America, Europe, and

North America (Table S2). However, the arboreal ecomorph dominates instead at some of the most species-rich tropical rainforest sites, including those in Africa, Madagascar, and both sites in South America (but not Borneo). Intriguingly, there were one or more independent origins of the arboreal ecomorph in each of these three regions. Furthermore, the arboreal ecomorph is associated with higher diversification rates whereas the other ecomorphs are not (Moen & Wiens, 2017). The other four ecomorphs (aquatic, burrowing, semi-aquatic, torrent-dwelling) tend to be much less frequent, especially in sites with high overall richness (>20 species). In many cases,

these ecomorphs also evolved in parallel among regions. Overall, patterns of ecomorph richness within many sites seem to be explained by the trait age hypothesis, whereas certain high-richness sites have independently come to be dominated by an ecomorph with higher diversification rates (arboreal). This latter result also raises the possibility that the higher diversification rate associated with this ecomorph may help explain patterns of overall local and regional species richness (see Section IV.7 below).

This case study is not a perfect example of trait-based richness patterns among parallel adaptive radiations. Not every species at every site is likely to be part of an adaptive radiation, nor are the clade compositions at each site completely independent (e.g. some clades are shared between sites). Nevertheless, it should illustrate the basic idea.

(7) Will studying the origins of trait-based richness patterns help reveal the causes of other richness patterns?

Focusing on the causes of spatial patterns of trait-based richness might be important to understanding spatial richness patterns, even if one is not interested in trait-based richness patterns for their own sake. There is already abundant evidence that traits can influence diversification rates of clades, and that diversification rates strongly influence their species richness (review in Wiens, 2017). We also know that traits can vary geographically (e.g. Bennie *et al.*, 2014; Moeller *et al.*, 2017). Therefore, many spatial patterns of richness might arise through an interaction between traits and diversification over space (e.g. if species in the tropics have higher diversification rates because of states present only in tropical species). Constraints on dispersal related to certain traits might also strongly influence spatial richness (e.g. lineages with certain states that are problematic for survival in temperate climates; Zanne *et al.*, 2014). Such constraints could lower dispersal rates to certain locations or cause those locations to be successfully colonised only recently (both potentially contributing to lower richness).

Here I give one example of a spatial richness pattern that is significantly associated with trait-based richness. The case study in frogs above (Fig. 8) shows substantial spatial variation in species richness and the relative frequencies of ecomorphs among sites, including a roughly fivefold variation in overall richness among the tropical sites. The sites with the highest overall frog richness have the highest proportion of arboreal species, and a non-parametric Spearman's rank test shows a significant positive correlation (Fig. 8C; $\rho = 0.756$; $P = 0.011$, $n = 10$ sites, in R version 3.6.3). Again, the higher richness of arboreal species appears to be related to faster diversification rates in arboreal lineages (Moen & Wiens, 2017). Intriguingly, there is not a significant correlation between latitude and overall richness ($\rho = -0.298$; $P = 0.403$) nor between latitude and the proportion of arboreal species ($\rho = -0.176$; $P = 0.626$). Thus, considering trait-based richness may help explain large-scale

variation in frog species richness that cannot be explained by latitude alone.

(8) Are trait-based richness patterns relevant to other questions?

Analysing trait-based richness patterns may help address many other questions in ecology, evolutionary biology, and conservation biology. For example, there has been considerable research on whether higher species richness makes communities more or less invulnerable by introduced species (e.g. Levine & D'Antonio, 1999). But (as with ecosystem function) the richness of species with different traits in each community might be more important in determining whether a community can be invaded or not, especially by introduced species with a given trait(s). More broadly, community assembly (and community restoration) may depend on the traits of species (HilleRisLambers *et al.*, 2012), and so considering the richness of species with each trait (or combination of traits) may be crucial. Of course, this may depend on the trait, and numerous other factors.

Perhaps most importantly, considering trait-based richness may lead to new questions. As just one example, consider the species richness of all the species that depend on a given host species (e.g. parasites, mutualists, commensals). One can ask whether a host species harbours more species with which their interactions have positive fitness effects for the host (e.g. mutualists) than those with negative fitness effects (e.g. parasites). We might predict this because species interactions with positive fitness effects for a given focal species seem to increase their diversification rates (Zeng & Wiens, 2021b), and seem to last longer (although not in animals; Zeng & Wiens, 2021a). Both factors should tend to increase richness (Figs 3 and 5). On the other hand, these patterns of species richness on hosts might instead be dominated by transition rates, with many short-lived parasitic interactions and fewer long-lasting positive interactions. Of course, many previous studies have considered the richness of parasites on hosts (e.g. Poulin & Morand, 2000) and the impacts of mutualism on species richness (e.g. Chomicki *et al.*, 2019), but not necessarily the relative richness of species associated with different types of interactions (i.e. trait-based richness) on a given host species. This is just one example.

X. CONCLUSIONS

(1) A major goal of ecology and evolutionary biology is to explain patterns of species richness, especially patterns among locations and among clades. Here, I have highlighted a third kind of richness pattern: different numbers of species with different trait values. These trait-based richness patterns can range from mammalian body-size distributions to the paradox of sex across living organisms. Although many studies have documented trait-based richness patterns, their causes remain underexplored, and a general

framework for explaining their origins has been lacking. Understanding their origins requires integrating ecology and macroevolution.

(2) Three hypotheses can directly explain patterns of trait-based richness within a given group of organisms. These are the diversification rate hypothesis (i.e. the most species-rich state proliferated more rapidly than other states), trait origins hypothesis (more evolutionary transitions to the most species-rich state), and trait age hypothesis (the most species-rich state evolved earlier than the other states).

(3) A systematic review suggests that the most broadly important of these three hypotheses for explaining trait-based richness patterns is the trait age hypothesis (i.e. the most species-rich state is the one that evolves first), more so than differences in diversification rates among states (which numerous studies have focused on instead). Although many details regarding the origins of trait-based richness patterns will doubtless vary among traits and organisms, these results suggest that general patterns might nevertheless emerge. Intriguingly, these results from trait-based studies parallel studies of spatial richness patterns in showing the importance of time over diversification rates and transition rates. These shared patterns hint at generalities that span diverse types of richness patterns.

(4) There may be consequences to ignoring trait-based richness patterns. For example, many prominent studies of spatial richness patterns in plants have included only woody species. This is actually a trait-based richness pattern, and such studies have often ignored the potential role of the timing and number of transitions between the woody and non-woody states in explaining these richness patterns.

(5) Trait-based richness may be relevant to many different topics in ecology and evolution, including adaptive radiation, biogeography, community saturation, ecosystem function, invasive species, and host–parasite relationships. I describe numerous unanswered questions related to trait-based richness patterns, their origins, and what they can tell us about other topics. For example, I show how spatial richness patterns in frogs may be related to the relative richness of the arboreal (treefrog) ecomorph, with the most species-rich locations having higher frequencies of arboreal species.

XI. ACKNOWLEDGEMENTS

I thank Michael Donoghue, Deborah Goldberg, Cody Howard, and two anonymous reviewers for helpful comments.

XII. REFERENCES

References identified with an asterisk (*) are cited only within the supporting information.

ADAMS, D. C. & COLLYER, M. L. (2018). Phylogenetic ANOVA: group-clade aggregation, biological challenges, and a refined permutation procedure. *Evolution* **72**, 1204–1215.

- AGUIAR, A. J. C., MELO, G. A. R., VASCONCELOS, T. N. C., GONÇALVES, R. B., GIUGLIANO, L. & MARTINS, A. C. (2020). Biogeography and early diversification of Tapinotaspini oil-bees support presence of Paleocene savannas in South America. *Molecular Phylogenetics and Evolution* **143**, 106692.
- ANDERSON, S. R. & WIENS, J. J. (2017). Out of the dark: 350 million years of conservatism and evolution in diel activity patterns in vertebrates. *Evolution* **71**, 1944–1959.
- BARIDO-SOTTANI, J., VAUGHAN, T. G. & STADLER, T. (2020). A multitype birth–death model for Bayesian inference of lineage-specific birth and death rates. *Systematic Biology* **69**, 973–986.
- BEAULIEU, J. M. & O'MEARA, B. C. (2016). Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Systematic Biology* **65**, 583–601.
- BEAULIEU, J. M., O'MEARA, B. C. & DONOGHUE, M. J. (2013). Identifying hidden rate changes in the evolution of a binary morphological character: the evolution of plant habit in campanulid angiosperms. *Systematic Biology* **62**, 725–737.
- BELL, G. (1982). *The Masterpiece of Nature. The Evolution and Genetics of Sexuality*. University of California Press, Berkeley, CA.
- BENNIE, J. J., DUFFY, J. P., INGER, R. & GASTON, K. J. (2014). Biogeography of time partitioning in mammals. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 13727–13732.
- BLACKBURN, T. M. & GASTON, K. J. (1994). The distribution of body sizes of the world's bird species. *Oikos* **70**, 127–130.
- BROWN, J. H. (2014). Why are there so many species in the tropics? *Journal of Biogeography* **41**, 8–22.
- BROWN, J. H. & MAURER, B. A. (1989). Macroecology – the division of food and space among species on the continents. *Science* **243**, 1145–1150.
- BURIN, G., KISSLING, W. D., GUIMARAES, P. R., SEKERCIOGLU, C. H. & QUENTAL, T. B. (2016). Omnivory in birds is a macroevolutionary sink. *Nature Communications* **7**, 11250.
- BURKE, N. W. & BONDURIANSKY, R. (2017). Sexual conflict, facultative asexuality, and the true paradox of sex. *Trends in Ecology and Evolution* **32**, 646–652.
- CHEN, Z. & WIENS, J. J. (2020). The origins of acoustic communication in vertebrates. *Nature Communications* **11**, 369.
- CHEN, L. & WIENS, J. J. (2021). Multicellularity and sex helped shape the tree of life. *Proceedings of the Royal Society of London Series B: Biological Sciences* **288**(2021), 1265.
- CHOMICKI, G., WEBER, M., ANTONELLI, A., BASCOMPTE, J. & KIERS, E. T. (2019). The impact of mutualisms on species richness. *Trends in Ecology and Evolution* **34**, 698–711.
- CRAVEN, D., KNIGHT, T. M., BARTON, K. E., BIALIC-MURPHY, L. & CHASE, J. M. (2019). Dissecting macroecological and macroevolutionary patterns of forest biodiversity across the Hawaiian archipelago. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 16436–16441.
- *CUNNINGHAM, C. W., OMLAND, K. E. & OAKLEY, T. H. (1998). Reconstructing ancestral character states: a critical reappraisal. *Trends in Ecology and Evolution* **13**, 361–366.
- CYRIAC, V. P. & KODANDARAMAIAH, U. (2018). Digging their own macroevolutionary grave: fossoriality as an evolutionary dead end in snakes. *Journal of Evolutionary Biology* **31**, 587–598.
- *DÁTILLO, W., BARROZO-CHÁVEZ, N., LIRA-NORIEGA, A., GUEVARA, R., VILLALOBOS, F., SANTIAGO-ALARCON, D., NEVES, F. S., IZZO, T. & RIBEIRO, S. P. (2020). Species-level drivers of mammalian ectoparasite faunas. *Journal of Animal Ecology* **89**, 1754–1765.
- DAVIS, M. P., MIDFORD, P. E. & MADDISON, W. (2013). Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. *BMC Evolutionary Biology* **13**, 38.
- DI VINCENZO, V., GRUENSTAEUDL, M., NAUHEIMER, L., WONDAFRASH, M., KAMAU, P., DEMISSEW, S. & BORSCH, T. (2018). Evolutionary diversification of the African achyranthoid clade (Amaranthaceae) in the context of sterile flower evolution and epizoochory. *Annals of Botany* **122**, 69–85.
- DONOGHUE, M. J., EATON, D. A. R., MAYA-LASTRA, C. A., LANDIS, M. J., SWEENEY, P. W., OLSON, M. E., IVALÚ CACHO, N., MOEGLEIN, M. K., GARDNER, J. R., HEAPHY, N. M., CASTORENA, M., SEGOVIA RIVAS, A., CLEMENT, W. L. & EDWARDS, E. J. (2022). Replicated radiation of a plant clade along a cloud forest archipelago. *Nature Ecology and Evolution* **6**, 1318–1329.
- EBERLE, J., DIMITROV, D., VALDEZ-MONDRAGÓN, A. & HUBER, B. A. (2018). Microhabitat change drives diversification in pholcid spiders. *BMC Evolutionary Biology* **18**, 141.
- EHRLICH, P. R. & RAVEN, P. H. (1964). Butterflies and plants: a study in coevolution. *Evolution* **18**, 586–608.
- ELTON, C. (1950). *The Ecology of Animals*. Methuen, London.
- FERNÁNDEZ-MAZUECOS, M., BLANCO-PASTOR, J. L., JUAN, A., CARNICERO, P., FORREST, A., ALARCÓN, M., VARGAS, P. & GLOVER, B. J. (2019). Macroevolutionary dynamics of nectar spurs, a key evolutionary innovation. *New Phytologist* **222**, 1123–1138.
- FINE, P. V. A. (2015). Ecological and evolutionary drivers of geographic variation in species diversity. *Annual Review of Ecology, Evolution, and Systematics* **46**, 369–392.

- FITZJOHN, R. G. (2010). Quantitative traits and diversification. *Systematic Biology* **59**, 619–633.
- FITZJOHN, R. G. (2012). Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution* **3**, 1084–1092.
- FITZJOHN, R. G., MADDISON, W. P. & OTTO, S. P. (2009). Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology* **58**, 595–611.
- FONTANETO, D., TANG, C. Q., OBERTEGGER, U., LEASI, F. & BARRACLOUGH, T. G. (2012). Different diversification rates between sexual and asexual organisms. *Evolutionary Biology* **39**, 262–270.
- FORBES, A. A., DEVINE, S. N., HIPPEE, A. C., TVEDTE, E. S., WARD, A. K. G., WIDMAYER, H. A. & WILSON, C. J. (2017). Revisiting the particular role of host shifts in initiating insect speciation. *Evolution* **71**, 1126–1137.
- FREYMAN, W. A. & HOHNA, S. (2019). Stochastic character mapping of state-dependent diversification reveals the tempo of evolutionary decline in self-compatible Onagraceae lineages. *Systematic Biology* **68**, 505–519.
- FURNESS, A. I., AVISE, J. C., POLLUX, B. J. A., REYNOSO, Y. & REZNICK, D. N. (2021). The evolution of the placenta in poeciliid fishes. *Current Biology* **31**, 2004–2011.
- GASTON, K. J. & BLACKBURN, T. M. (2000). *Pattern and Process in Macroecology*. Blackwell Science, Oxford.
- GILLESPIE, R. G., BENNETT, G. M., DE MEESTER, L., FEDER, J. L., FLEISCHER, R. C., HARMON, L. J., HENDRY, A. P., KNOPE, M. L., MALLETT, J., MARTIN, C., PARENT, C. E., PATTON, A. H., PFENNIG, K. S., RUBINOFF, D., SCHLUTER, D., *ET AL.* (2020). Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity* **111**, 1–20.
- GLOR, R. E. (2010). Phylogenetic insights on adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* **41**, 251–270.
- GOODWILLIE, C., SARGENT, R. D., ECKERT, C. G., ELLE, E., GERBER, M. A., JOHNSTON, M. O., KALISZ, S., MOELLER, D. A., REE, R. H., VALLEJO-MARIN, M. & WINN, A. A. (2010). Correlated evolution of mating system and floral display traits in flowering plants and its implications for the distribution of mating system variation. *New Phytologist* **185**, 311–321.
- HARDY, N. B. & OTTO, S. P. (2014). Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. *Proceedings of the Royal Society of London Series B: Biological Sciences* **281**, 20132960.
- HARMON, L. J. & HARRISON, S. P. (2015). Species diversity is dynamic and unbounded at local and regional scales. *American Naturalist* **185**, 584–593.
- HARRINGTON, S. M., DE HAAN, J. M., SHAPIRO, L. & RUANE, S. (2018). Habits and characteristics of arboreal snakes worldwide: arboreality constrains body size but does not affect lineage diversification. *Biological Journal of the Linnean Society* **125**, 61–71.
- HEIM, N. A., KNOPE, M. L., SCHAAL, E. K., WANG, S. C. & PAYNE, J. L. (2015). Cope's rule in the evolution of marine animals. *Science* **347**, 867–870.
- HILLEBRAND, H. (2004). On the generality of the latitudinal diversity gradient. *American Naturalist* **163**, 192–211.
- HILLERISLAMBERS, J., ADLER, P. B., HARPOLE, W. S., LEVINE, J. M. & MAYFIELD, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* **43**, 227–248.
- HOEHNA, S., FREYMAN, W. A., NOLEN, Z., HUELSENBECK, J., MAY, M. R. & MOORE, B. R. (2019). A Bayesian approach for estimating branch-specific speciation and extinction rates. *bioRxiv*. <https://doi.org/10.1101/555805>.
- HOOPER, D. U., CHAPIN, F. S. III, EWEL, J. J., HECTOR, A., INCHAUSTI, P., LAVOREL, S., LAWTON, J. H., LODGE, D. M., LOREAU, M., NAEEM, S., SCHMID, B., SETÄLÄ, H., SYMSTAD, A. J., VANDERMEER, J. & WARDLE, D. A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* **75**, 3–35.
- HOWARD, C. C., LANDIS, J. B., BEAULIEU, J. M. & CELLINESE, N. (2020). Geophytism in monocots leads to higher rates of diversification. *New Phytologist* **225**, 1023–1032.
- HUELSENBECK, J. P., NIELSEN, R. & BOLLBACK, J. P. (2003). Stochastic mapping of morphological characters. *Systematic Biology* **52**, 131–138.
- HUTCHINSON, G. E. & MACARTHUR, R. H. (1959). A theoretical ecological model of size distributions among species of animals. *American Naturalist* **93**, 117–125.
- HUTTER, C. R., GUAYASAMIN, J. M. & WIENS, J. J. (2013). Explaining Andean megadiversity: the evolutionary and ecological causes of glassfrog elevational richness patterns. *Ecology Letters* **16**, 1135–1144.
- IGEA, J. & TANENTZAP, A. J. (2020). Angiosperm speciation cools down in the tropics. *Ecology Letters* **3**, 692–700.
- IVES, A. R. & GARLAND, T. (2010). Phylogenetic logistic regression for binary dependent variables. *Systematic Biology* **59**, 9–26.
- JABLONSKI, D. (1997). Body-size evolution in Cretaceous molluscs and the status of Cope's rule. *Nature* **385**, 250–252.
- JANSSON, R., RODRIGUEZ-CASTANEDA, G. & HARDING, L. E. (2013). What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution* **67**, 1741–1755.
- JETZ, W., THOMAS, G., JOY, J., HARTMANN, K. & MOEERS, A. (2012). The global diversity of birds in space and time. *Nature* **491**, 444–448.
- JONES, K. E. & PURVIS, A. (1997). An optimum body size for mammals? Comparative evidence from bats. *Functional Ecology* **11**, 751–756.
- *KAMIYA, T., O'DWYER, K., NAKAGAWA, S. & POULIN, R. (2014). What determines species richness of parasitic organisms? A meta-analysis across animal, plant and fungal hosts. *Biological Reviews* **89**, 123–134.
- KERKHOFF, A. J., MORIARITY, P. E. & WEISER, M. D. (2014). The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 8125–8130.
- KOZLOWSKI, J. & GAWELCZYK, A. (2002). Why are species' body size distributions usually skewed to the right? *Functional Ecology* **16**, 419–431.
- KRAFT, N. J. B., GODOY, O. & LEVINE, J. M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 797–802.
- KRATINA, P., LECRAW, R. M., INGRAM, T. & ANHOLT, B. R. (2012). Stability and persistence of food webs with omnivory: is there a general pattern? *Ecosphere* **3**, 1–18.
- LAENEN, B., MACHAC, A., GRADSTEIN, S. R., SHAW, B., PATINO, J., DÉSAMORÉ, A., GOFFINET, B., COX, C. J., SHAW, A. J. & VANDERPOORTEN, A. (2016). Increased diversification rates follow shifts to bisexuality in liverworts. *New Phytologist* **210**, 1121–1129.
- LANDIS, M. J., MATZKE, N. J., MOORE, B. R. & HUELSENBECK, J. P. (2013). Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology* **62**, 789–804.
- LANDIS, J. B., BELL, C. D., HERNANDEZ, M., ZENIL-FERGUSON, R., MCCARTHY, E. W., SOLTIS, D. E. & SOLTIS, P. S. (2018). Evolution of floral traits and impact of reproductive mode on diversification in the phlox family (Polemoniaceae). *Molecular Phylogenetics and Evolution* **127**, 878–890.
- LETSCH, H., GOTTSBERGER, B., METZL, C., ASTRIN, J., FRIEDMAN, A. L. L., MCKENNA, D. D. & FIEDLER, K. (2018). Climate and host-plant associations shaped the evolution of ceutorhynch weevils throughout the Cenozoic. *Evolution* **72**, 1815–1828.
- LEVINE, J. M. (2016). A trail map for trait-based studies. *Nature* **529**, 163–164.
- LEVINE, J. M. & D'ANTONIO, C. M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15–26.
- LI, H. & WIENS, J. J. (2019). Time explains regional richness patterns within clades more often than diversification rates or area. *American Naturalist* **193**, 514–529.
- LIEDTKE, H. C., WIENS, J. J. & GOMEZ-MESTRE, I. (2022). The evolution of reproductive modes and life cycles in amphibians. *Nature Communications* **13**, 7039.
- LOREAU, M., NAEEM, S., INCHAUSTI, P., BENTGSSON, J., GRIME, J. P., HECTOR, A., HOOPER, D. U., HUSTON, M. A., RAFFAELLI, D., SCHMID, B., TILMAN, D. & WARDLE, D. A. (2001). Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**, 804–808.
- LOSOS, J. B., JACKMAN, T. R., LARSON, A., DE QUEIROZ, K. & RODRÍGUEZ-SCHETTINO, L. (1998). Historical contingency and determinism in replicated adaptive radiations of Island lizards. *Science* **279**, 2115–2118.
- LOUCA, S. & PENNELL, M. W. (2020). Extant timetrees are consistent with a myriad of diversification histories. *Nature* **580**, 502–505.
- MACARTHUR, R. H. & WILSON, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution* **17**, 373–387.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton University Press, NJ.
- MADDISON, W. P., MIDFORD, P. E. & OTTO, S. P. (2007). Estimating a binary character's effect on speciation and extinction. *Systematic Biology* **56**, 701–710.
- MADDISON, W. P. & FITZJOHN, R. G. (2015). The unsolved challenge to phylogenetic correlation tests for categorical characters. *Systematic Biology* **64**, 127–136.
- MALLET, O., HARTIG, F. & MORLON, H. (2019). A model with many small shifts for estimating species-specific diversification rates. *Nature Ecology and Evolution* **3**, 1086–1092.
- MAURER, B. A. & BROWN, J. H. (1988). Distribution of energy use and biomass among species of North American terrestrial birds. *Ecology* **69**, 1923–1932.
- MAURER, B. A., BROWN, J. H. & RUSLER, R. D. (1992). The micro and macro in body size evolution. *Evolution* **46**, 939–953.
- MAYNARD SMITH, J. (1978). *The Evolution of Sex*. Cambridge University Press, New York.
- MCGILL, B. J., ENQUIST, B. J., WEIHER, E. & WESTOBY, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**, 178–185.
- MCGILL, B. J., CHASE, J. M., HORTAL, J., OVERCAST, I., ROMINGER, A. J., ROSINDELL, J., BORGES, P. A. V., EMERSON, ETIENNE, R. S., HICKERSON, M. J., MAHLER, D. L., MASSOL, F., MCGAUGHAN, A., NEVES, P., PARENT, C., *ET AL.* (2019). Unifying macroecology and macroevolution to answer fundamental questions about biodiversity. *Global Ecology and Biogeography* **28**, 1925–1936.
- MCPEEK, M. A. & BROWN, J. M. (2007). Clade age and not diversification rate explains species richness among animal taxa. *American Naturalist* **169**, E97–E106.

- MESSIER, J., MCGILL, B. J. & LECHOWIZ, M. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* **13**, 838–848.
- MILLER, E. C. & WIENS, J. J. (2017). Extinction and time help drive the marine-terrestrial biodiversity gradient: is the ocean a deathtrap? *Ecology Letters* **20**, 911–921.
- MITTELBACH, G. G., SCHEMSKE, D. W., CORNELL, H. V., ALLEN, A. P., BROWN, J. M., BUSH, M. B., HARRISON, S. P., HURLBERT, A. H., KNOWLTON, N., LESSIOS, H. A., MCCAIN, C. M., MCCUNE, A. R., MCDADE, L. A., MCPEEK, M. A., NEAR, T. J., *ET AL.* (2007). Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10**, 315–331.
- MOELLER, D. A., RUNQUIST, R. D. B., MOE, A. M., GEBER, M. A., GOODWILLIE, C., CHEPTOU, P.-O., ECKERT, C. G., ELLE, E., JOHNSTON, M. O., KALISZ, S., REE, R. H., SARGENT, R. D., VALLEJO-MARIN, M. & WINN, A. A. (2017). Global biogeography of mating system variation in seed plants. *Ecology Letters* **20**, 375–384.
- MOEN, D. S., MORLON, H. & WIENS, J. J. (2016). Testing convergence versus history: convergence dominates phenotypic evolution for over 150 million years in frogs. *Systematic Biology* **65**, 146–160.
- MOEN, D. S. & WIENS, J. J. (2017). Microhabitat and climatic-niche change explain patterns of diversification among frog families. *American Naturalist* **190**, 29–44.
- MOREIRA, M. O., FONSECA, C. & ROJAS, D. (2021). Parthenogenesis is self destructive for scaled reptiles. *Biology Letters* **17**, 20210006.
- MORLON, H. (2014). Phylogenetic approaches for studying diversification. *Ecology Letters* **17**, 508–525.
- NAEEM, S., DUFFY, J. E. & ZAVALETA, E. (2012). The functions of biological diversity in an age of extinction. *Science* **331**, 1401–1406.
- NAKOV, T., BEAULIEU, J. M. & ALVERSON, A. J. (2019). Diatoms diversify and turn over faster in freshwater than marine environments. *Evolution* **73**, 2497–2511.
- NEIMAN, M., LIVELY, C. M. & MEIRMAN, S. (2017). Why sex? A pluralist approach revisited. *Trends in Ecology and Evolution* **32**, 589–600.
- NEUPANE, S., LEWIS, P. O., DESSEIN, S., SHANKS, H., PAUDYAL, S. & LENS, F. (2017). Evolution of woody life form on tropical mountains in the tribe Spermaceae (Rubiaceae). *American Journal of Botany* **104**, 419–438.
- NOSIL, P. (2012). *Ecological speciation*. Oxford University Press, Oxford.
- O'MEARA, B. C., SMITH, S. D., ARMBRUSTER, W. S., HARDER, L. D., HARDY, C. R., HILEMAN, L. R., HUFFORD, L., LITT, A., MAGALLÓN, S., SMITH, S. A., STEVENS, P. F., FENSTER, C. B. & DIGGLE, P. K. (2016). Non-equilibrium dynamics and floral trait interactions shape extant angiosperm diversity. *Proceedings of the Royal Society of London Series B: Biological Sciences* **283**, 20152304.
- ORD, T. J. & COOKE, G. M. (2016). Repeated evolution of amphibious behavior in fish and its implications for the colonization of novel environments. *Evolution* **70**, 1747–1759.
- OTERO, A., JIMÉNEZ-MEJÍAS, P., VALCÁRCEL, V. & VARGAS, P. (2020). Being in the right place at the right time? Parallel diversification bursts favored by the persistence of ancient epizoochorous traits and hidden factors in Cynoglossoidae. *American Journal of Botany* **106**, 438–452.
- OTTO, S. P. & LENORMAND, T. (2002). Evolution of sex: resolving the paradox of sex and recombination. *Nature Reviews Genetics* **3**, 252–261.
- PAGEL, M. (1994). Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London Series B: Biological Sciences* **255**, 37–45.
- PAGEL, M., MEADE, A. & BARKER, D. (2004). Bayesian estimation of ancestral character states on phylogenies. *Systematic Biology* **53**, 673–684.
- PAGEL, M. & MEADE, A. (2022). *BayesTraits, version 4*. University of Reading, Berkshire <http://www.evolution.rdg.ac.uk>.
- PIANKA, E. (1966). Latitudinal gradients in species diversity: A review of concepts. *American Naturalist* **100**, 33–46.
- PONTARP, M. & WIENS, J. J. (2017). The origin of species richness patterns along environmental gradients: uniting explanations based on time, diversification rate, and carrying capacity. *Journal of Biogeography* **44**, 722–735.
- PORTIK, D. M., BELL, R. C., BLACKBURN, D. C., BAUER, A. M., BARRATT, C. D., BRANCH, W. R., BURGER, M., CHANNING, A., COLSTON, T. J., CONRADIE, W., DEHLING, J. M., DREWES, R. C., ERNST, R., GREENBAUM, E., GVOZDÍK, V., *ET AL.* (2019). Sexual dichromatism drives diversification within a major radiation of African amphibians. *Systematic Biology* **68**, 859–875.
- POULIN, R. P. & MORAND, S. (2000). The diversity of parasites. *Quarterly Review of Biology* **75**, 277–293.
- PREBUS, M. (2017). Insights into the evolution, biogeography and natural history of the acorn ants, genus *Tenothorax* Mayr (Hymenoptera: Formicidae). *BMC Evolutionary Biology* **17**, 250.
- PRICE, S. A., HOPKINS, S. S. B., SMITH, K. K. & ROTH, V. L. (2012). Tempo of trophic evolution and its impact on mammalian diversification. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 7008–7012.
- QIAN, H., WIENS, J. J., ZHANG, J. & ZHANG, Y. (2015). Evolutionary and ecological causes of species richness patterns in North American angiosperm trees. *Ecography* **38**, 241–250.
- RABOSKY, D. L. (2010). Extinction rates should not be estimated from molecular phylogenies. *Evolution* **64**, 1816–1824.
- RABOSKY, D. L. & GOLDBERG, E. E. (2015). Model inadequacy and mistaken inferences of trait-dependent speciation. *Systematic Biology* **64**, 340–355.
- RABOSKY, D. L., CHANG, J., TITLE, P. O., COWMAN, P. F., SALLAN, L., FRIEDMAN, M., KASCHNER, K., GARILAO, C., NEAR, T. J., COLL, M. & ALFARO, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature* **559**, 392–395.
- REE, R. H. & SMITH, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* **57**, 4–14.
- REGINATO, M., VASCONCELOS, T. N. C., KRIEBEL, R. & SIMÕES, A. O. (2020). Is dispersal mode a driver of diversification and geographical distribution in the tropical plant family Melastomataceae? *Molecular Phylogenetics and Evolution* **148**, 106815.
- REVELL, L. J. (2014). Ancestral character estimation under the threshold model from quantitative genetics. *Evolution* **68**, 743–759.
- RICKLEFS, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science* **235**, 167–171.
- RICKLEFS, R. E. (2006). Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology* **87**, S3–S13.
- RIVKIN, L. R., CASE, A. L. & CARUSO, C. M. (2016). Why is gynodioecy a rare but widely distributed sexual system? Lessons from the Lamiaceae. *New Phytologist* **211**, 688–696.
- ROMÁN-PALACIOS, C., SCHOLL, J. P. & WIENS, J. J. (2019). Evolution of diet across the animal tree of life. *Evolution Letters* **3**, 339–347.
- SCHLUTER, D. (2000). *The Ecology of Adaptive Radiation*. Oxford University Press, Oxford.
- SCHLUTER, D. (2016). Speciation, ecological opportunity, and latitude: (American Society of Naturalists address). *American Naturalist* **187**, 1–18.
- *SCHLUTER, D., PRICE, T., MOOERS, A. Ø. & LUDWIG, D. (1997). Likelihood of ancestor states in adaptive radiation. *Evolution* **51**, 1699–1711.
- SCHOLL, J. P. & WIENS, J. J. (2016). Diversification rates and species richness across the tree of life. *Proceedings of the Royal Society of London Series B: Biological Sciences* **283**, 20161335.
- SCOTLAND, R. W. & SANDERSON, M. J. (2004). The significance of few versus many in the tree of life. *Science* **303**, 643.
- SEEHAUSEN, O. (2006). African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society of London Series B: Biological Sciences* **273**, 1987–1998.
- SEGOVIA, R. A., PENNINGTON, R. T., BAKER, T. R., COELHO DE SOUZA, F., NEVES, D. M., DAVIS, C. C., ARMESTO, J. J., OLIVERA-FILHO, A. T. & DEXTER, K. G. (2020). Freezing and water availability structure the evolutionary diversity of trees across the Americas. *Science Advances* **6**, eaaz5373.
- SERRANO-SERRANO, M. L., ROLLAND, J., CLARK, J. L., SALAMIN, N. & PERRET, M. (2017). Hummingbird pollination and the diversification of angiosperms: an old and successful association in Gesneriaceae. *Proceedings of the Royal Society of London Series B: Biological Sciences* **284**, 20162816.
- SMAERS, J. B., MONGLE, C. S. & KANDLER, A. (2016). A multiple variance Brownian motion framework for the estimation of ancestral states and rates of evolution. *Biological Journal of the Linnean Society* **118**, 78–94.
- SONG, H., BÉTHOUX, O., SHIN, S., DONATH, A., LETSCH, H., LIU, S., MCKENNA, D. D., MENG, G., MISOF, B., POSIADŁOWSKI, L., ZHOU, X., WIPFLER, B. & SIMON, S. (2020). Phylogenomic analysis sheds light on the evolutionary pathways towards acoustic communication in Orthoptera. *Nature Communications* **11**, 4939.
- STEPHENS, P. R. & WIENS, J. J. (2003). Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *American Naturalist* **161**, 112–128.
- STROUD, J. T. & LOSOS, J. B. (2016). Ecological opportunity and adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics* **47**, 507–532.
- TERBORGH, J. W. & FAARBORG, J. (1980). Saturation of bird communities in the West Indies. *American Naturalist* **116**, 178–195.
- TILMAN, D. (2011). Diversification, biotic interchange, and the universal trade-off hypothesis. *American Naturalist* **178**, 355–371.
- TILMAN, D., KNOPS, J., WEDIN, D., REICH, P., RITCHIE, M. & SIEMANN, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science* **277**, 1300–1302.
- VASCONCELOS, T., O'MEARA, B. C. & BEAULIEU, J. M. (2022). A flexible method for estimating tip diversification rates across a range of speciation and extinction scenarios. *Evolution* **76**, 1420–1433.
- VIOLLE, C., REICH, P. B., PACALA, S. W., ENQUIST, B. J. & KATTGE, J. (2014). The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 13690–13696.
- WEBER, M. G. & AGRAWAL, A. (2014). Defense mutualisms enhance plant diversification. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 16442–16447.

- WESSINGER, C. A., RAUSHER, M. D. & HILEMAN, L. C. (2019). Adaptation to hummingbird pollination is associated with reduced diversification in *Penstemon*. *Evolution Letters* **3**, 521–533.
- WIENS, J. J. (2017). What explains patterns of biodiversity across the tree of life? *BioEssays* **39**, 1600128.
- *WIENS, J. J., KUCZYNSKI, C., DUELLMAN, W. E. & REEDER, T. W. (2007). Loss and re-evolution of complex life cycles in marsupial frogs: can ancestral trait reconstruction mislead? *Evolution* **61**, 1886–1899.
- WILLIAMS, G. C. (1975). *Sex and Evolution*. Princeton University Press, Princeton.
- XUE, B., GUO, X., LANDIS, J. B., SUN, M., TANG, C. C., SOLTIS, P. S., SOLTIS, D. E. & SAUNDERS, R. M. K. (2020). Accelerated diversification correlated with functional traits shapes extant diversity of the early divergent angiosperm family Annonaceae. *Molecular Phylogenetics and Evolution* **142**, 106659.
- YODER, J. B., CLANCEY, E., DES ROCHES, S., EASTMAN, J. M., GENTRY, L., GODSOE, W., HAGEY, T. J., JOCHIMSEN, D., OSWALD, B. P., ROBERTSON, J., SARVER, B. A. J., SCHENK, J. J., SPEAR, S. F. & HARMON, L. J. (2010). Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology* **23**, 1581–1596.
- ZANNE, A. E., TANK, D. C., CORNWELL, W. K., EASTMAN, J. M., SMITH, S. A., FITZJOHN, R. G., MCGLINN, D. J., O'MEARA, B. C., MOLES, A. T., REICH, P. B., ROYER, D. L., SOLTIS, D. E., STEVENS, P. F., WESTOBY, M., WRIGHT, I. J., *ET AL.* (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89–92.
- ZENG, Y. & WIENS, J. J. (2021a). Do mutualistic interactions last longer than antagonistic interactions? *Proceedings of the Royal Society of London Series B: Biological Sciences* **288**, 20211457.
- ZENG, Y. & WIENS, J. J. (2021b). Species interactions have predictable impacts on diversification. *Ecology Letters* **24**, 239–248.

XIII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Equilibrium *versus* non-equilibrium trait-based richness patterns.

Appendix S2. Testing the trait age hypothesis.

Appendix S3. Host–parasite richness.

Table S1. Trait-based richness patterns among clades in amphibians.

Table S2. Estimated relative richness of different frog ecomorphs at 10 sites.

(Received 7 November 2022; revised 21 March 2023; accepted 27 March 2023; published online 4 April 2023)