

## Review

# Speciation across life and the origins of biodiversity patterns

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### ABSTRACT

Speciation is the original source of all species richness. Here, I address two questions: (i) what might typical speciation look like across life? and (ii) how has speciation led to the diversity of life we see today? What is 'typical' depends on the richness of different groups. In groups associated with host organisms (which may dominate numerically), the processes of co-speciation and host switching are crucial. Among free-living organisms, allopatric speciation, ecological divergence, and prezygotic isolation appear widely important. Yet, the processes by which species become allopatric (and initially split) remain highly unclear. Among macroscopic organisms, the processes underlying the speciation of cryptic insect lineages may predominate, and are briefly reviewed here. Analyses of diversification rates among clades can illuminate the factors that drive speciation and species richness, and I review the advantages and disadvantages of different methods for estimating diversification rates. Patterns of species richness among named clades are generally related to variation in diversification rates, and specific types of ecological variables seem to underlie variation in diversification rates at different scales. Nevertheless, many richness patterns are unrelated to diversification rates and may be related to the time available for speciation instead, including richness among regions, clades, and traits.

**Keywords:** biodiversity; co-speciation; diversification; host switching; niche conservatism; macroevolution; phylogeny; speciation; species richness

### INTRODUCTION

Speciation is a fundamental process in biology. It is the source of all species and thus the overall diversity of life. It also underlies many patterns of species richness, such as the latitudinal diversity gradient, the dominance of angiosperms among land plants and of arthropods among animals, and the preponderance of sexual reproduction among eukaryotes.

In this review, I will address two main questions. First, what might typical speciation be like across life? Second, how has speciation led to the diversity of life that we see today? Of course, each of these topics could be the basis for multiple review papers. For the first part, I will emphasize some basic aspects of speciation that can be characterized broadly across organisms, including geographic modes, ecological divergence, isolating barriers, and host-associated divergence. I will also emphasize that what is typical across life depends on the species richness of different groups. For the second part, I will emphasize how we can use phylogenies to infer large-scale patterns of speciation and diversification and what these analyses tell us about the origins of species richness patterns.

These two main questions are broad, but they clearly do not address all of speciation research. Other contributions to this

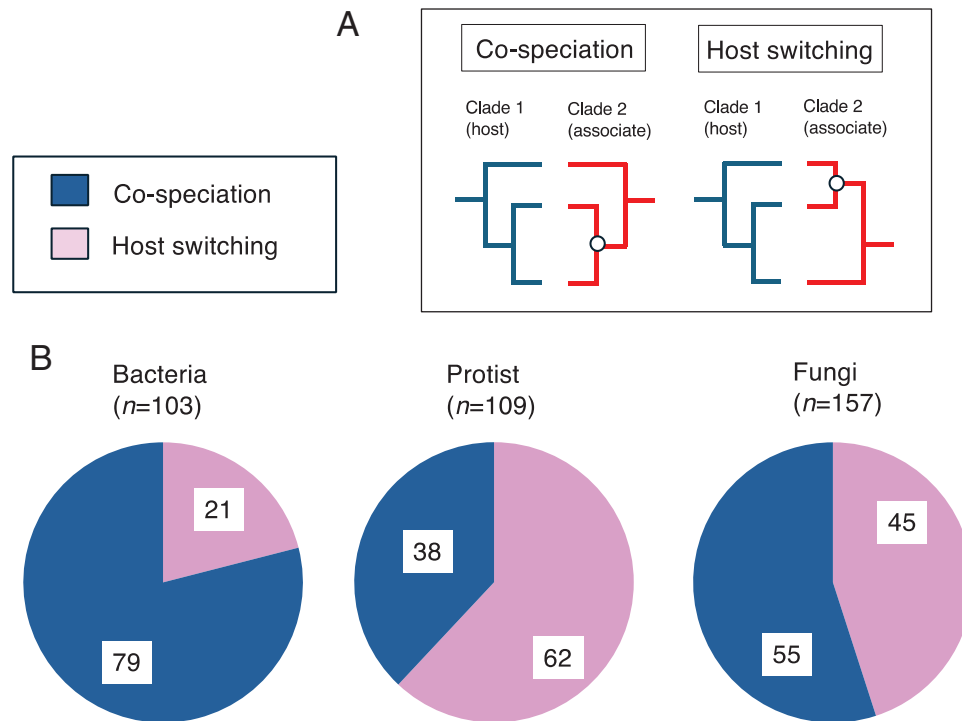
symposium will address many other major topics in speciation research (e.g. [Butlin and Faria 2024](#), [Dupré 2024](#), [Eiserhardt et al. 2024](#), [Singhal et al. 2024](#), [Stelkens et al. 2024](#)).

### TYPICAL SPECIATION

#### Overview

What is typical speciation across life? Here, I will lean on a recent synthesis ([Hernández-Hernández et al. 2021](#)). That paper focused on a limited number of topics but covered them across all major groups. I also emphasize two topics not covered there: how allopatry arises and speciation in cryptic insect species.

I focus primarily on sexually reproducing species. Many species concepts concur that genetic exchange among conspecifics is an important aspect of species, including the biological ([Wright 1940](#), [Mayr 1942](#), [Dobzhansky 1950](#)), evolutionary ([Simpson 1951](#), [Wiley 1978](#)), and general lineage concepts ([de Queiroz 1998, 2007](#)). These three concepts are the most widely used ([Stankowski and Ravinet 2021](#)). Bacteria lack sexual reproduction, but >90% of sampled bacterial species have genetic exchange among closely related individuals ([Diop et al. 2022](#)). Thus, most bacterial species may be comparable to eukaryotic



**Figure 1.** Speciation in host-associated organisms. A, simplified examples of co-speciation (left) and host-switching (right) in host-associated species, showing the phylogenies of three host species (blue) and their three host-associated species (red; parasites, mutualists, or commensals). In the example on the left, there is co-speciation (open circle) between the host and host-associated species, indicated by the congruent phylogenies between the host and host-associated species. In the example on the right, there is host-switching by the host-associated species, indicated by the incongruent node on the tree (open circle). B, the inferred frequencies of co-speciation (blue) and host-switching (pink) in bacteria, protists, and fungi. The number in white is the percentage of nodes consistent with each mechanism. The sample size in each group is the number of nodes from the empirical studies summarized in figure 1 of [Hernández-Hernández et al. \(2021\)](#). Note that these congruent and incongruent nodes are merely a ‘first-pass’ approach at estimating these frequencies.

species ([Fraser et al. 2007](#), [Shapiro et al. 2012](#), [Bobay and Ochman 2017](#)). There are asexual species in other groups (review in [Chen and Wiens 2021](#)) including archaeans, some fungi and animals, predominantly selfing land plants (~13% of Embryophyta species), and some algae (Glaucophyta, Chlorophyta) and protists (Choanozoa, Excavata, Filasterea, Katablepharidophyta). These asexual taxa have limited species numbers ([Chen and Wiens 2021](#)) but it is also unclear how to count them.

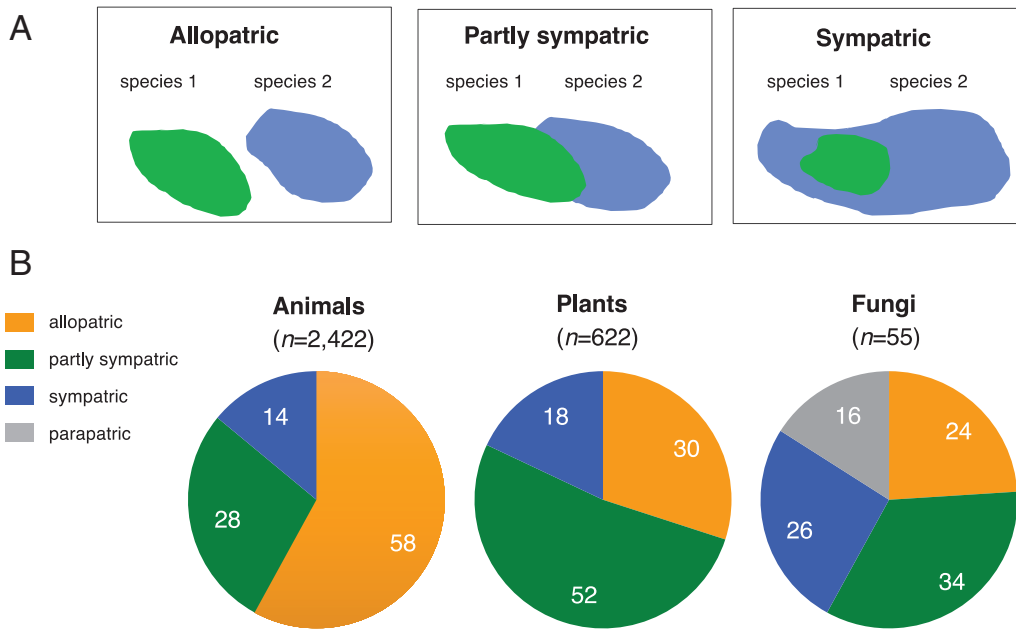
#### Speciation in free-living vs. host-associated organisms

Much of the speciation literature focuses on free-living species (e.g. [Coyne and Orr 2004](#)). However, free-living organisms may actually be in the minority when considering all species across life. For example, a review ([Larsen et al. 2017](#)) has suggested that each insect species may host (on average) approximately one species of apicomplexan protist (i.e. the group containing malaria-causing *Plasmodium*), one species of microsporidian fungi (i.e. unicellular parasites), and several bacteria species. Given that ~50% of known species are insects (~1 of 2 million species; [Bánki et al. 2024](#)), host-associated species may outnumber free-living ones many times over. Mites and nematodes may show similar patterns, with about one mite species per insect host species (on average) and one or more nematodes ([Larsen et al. 2017](#)). I use the agnostic term ‘host-associated’ here because these species could be parasites, commensals, or mutualists, depending on the group and species.

How do these host-associated organisms speciate? Much literature has focused on two processes (review in [de Vienne et al. 2013](#)). Co-speciation occurs when the host speciates and the host-associated species is split by the same process (e.g. allopatry). In the simplest case, this should lead to congruent nodes between the phylogenies of the host and host-associated species ([Fig. 1A](#)). Conversely, host-switching occurs when the host-associated species colonizes a new host, and under simple conditions, should lead to incongruent nodes of the host and associate phylogenies ([Fig. 1B](#)).

[Hernández-Hernández et al. \(2021\)](#) examined the relative frequencies of these processes in bacteria, protists (*sensu lato*), and fungi. They found >100 relevant speciation events in groups in which the host and host-associated phylogenies could be compared ([Fig. 1B](#)). Based on their results ([Fig. 1B](#)), co-speciation was predominant in bacteria (co-speciation: 79% vs. host-switching: 21%;  $N = 103$  nodes), host-switching was more common in protists (host-switching: 62% vs. co-speciation: 38%;  $N = 109$ ), whereas these frequencies were similar in fungi (co-speciation: 55%; host-switching: 45%;  $N = 157$ ).

Using congruence between the phylogenies of hosts and host-associated species is a ‘first-pass’ approach. Additional evidence is necessary to further test these mechanisms ([de Vienne et al. 2013](#)). Further, co-speciating hosts and their associated species need not split simultaneously, but instead may split in response to the same external factor (e.g. allopatry). Indeed it may



**Figure 2.** Geographic modes of speciation. A, simplified examples illustrating geographic ranges of sister species that are allopatric (geographically separated), partly sympatric (ranges of species 1 and 2 partly overlap), and fully sympatric (geographic range of species 1 is entirely within the range of species 2). B, frequencies of different patterns of range overlap of sister-species pairs in animals, plants, and fungi. These patterns of range overlap are essential for estimating geographic modes of speciation (Skeels and Cardillo 2019). Numbers in white are the percentages of each geographic pattern in each group. Sample size is the number of species pairs in each group. Data are from the empirical studies summarized in figure 2 of Hernández-Hernández *et al.* (2021). Note that sampling of animals is dominated by vertebrates ( $N = 1627$  pairs) but patterns are broadly similar between vertebrates and insects, marine invertebrates, and molluscs. For example, the frequency of allopatric pairs ranges from 53 to 77% among these four groups and sympatric pairs range from 10 to 25%. Parapatry is only treated as separate from partial sympatry in fungi, and is otherwise not illustrated here.

be difficult to conclude that splits occurred contemporaneously given the difficulty of precisely inferring absolute divergence times, especially in groups with limited fossil records (e.g. bacteria, protists, and fungi).

The larger point is that host-associated speciation is not necessarily treated as a central topic in speciation research. As one example, this topic is largely ignored in the classic book by Coyne and Orr (2004). However, host-associated speciation might be ‘typical speciation’ when counting all species across life. The extent to which host-associated speciation is similar to or different from that in free-living organisms (aside from the obvious ecological differences) remains an open question.

Not everyone may believe that host-associated species outnumber free-living ones. The evidence for their high richness comes from extrapolating a limited number of case studies that examined host-specific species among closely related insects (Larsen *et al.* 2017). Clearly this is an area in need of additional study, and is crucial for understanding typical speciation across life.

#### Generalities about speciation from free-living organisms

The review of Hernández-Hernández *et al.* (2021) made several generalities about speciation across life. First they found that allopatric speciation was probably the most frequent geographic mode in animals and plants (Fig. 2). This was inferred based largely on geographic overlap between pairs of sister-species, which can be used to estimate the initial geographic mode (Skeels and Cardillo 2019). Although it can be problematic to

infer sympatric speciation based on current sympatry alone, inferring that currently allopatric species were initially allopatric is less controversial. Species that were partially sympatric were considered ambiguous and were not included when estimating geographic modes (i.e. these might have been initially allopatric and become partially sympatric later, but this would require additional analyses, such as correlating range overlap and divergence times). I recognize that there is potentially a continuum between geographic modes based on levels of geographic overlap. Parapatry was not treated separately from partial sympatry in plants and animals and is not discussed.

Across animals, they (Hernández-Hernández *et al.* 2021) found that allopatric species pairs predominated in every group (>50%), including insects (59%;  $N = 231$  pairs), molluscs (77%;  $N = 276$  pairs), marine invertebrates (68%;  $N = 288$  pairs), and vertebrates (53%;  $N = 1627$  pairs). In plants (Fig. 2), allopatric pairs (30% of 622 pairs) outnumbered sympatric pairs (18%), but by a much smaller margin than in animals, and most species pairs were partially sympatric (52%). Fungi showed a pattern similar to plants (Fig. 2), with sympatric pairs slightly more common than allopatric pairs (26% vs. 24%;  $N = 55$  pairs), and partially sympatric pairs most common (34%). Each group (animals, plants, fungi) had a nontrivial number of sympatric pairs (10–26%). There were insufficient data to infer frequencies in protists, bacteria, and archaeans, but there was evidence suggesting allopatric speciation in bacteria and protists. Overall, these results put considerable data behind the idea that allopatric speciation is a common and widespread geographic mode

in animals, and possibly other groups. An interesting deviation is that sympatric pairs were more common in lacustrine fishes (96% of 21 pairs) and marine fishes (36% sympatric vs. 23% allopatric). These are environments with few obvious barriers to gene flow, especially lakes. Overall, these results are broadly concordant with previous estimates (e.g. [Skeels and Cardillo 2019](#)), in suggesting the predominance of allopatric speciation in animals (but with possibly more frequent sympatric speciation in plants and fungi).

Second, they concluded that ecological divergence was widespread, and probably broadly important in speciation. For example, they summarized evidence for ecological divergence between 80% of the sister-species pairs of insects with relevant data (89/111). Among those 89 pairs, 54% involved host shifts in herbivorous insects. However, these data come with the caveat that the selection of species for speciation research may not be unbiased. In molluscs, 62% of 29 marine sister-species pairs were ecologically divergent, but only 30% of 15 freshwater pairs were. In plants, ecological divergence was present between sister species in 65–80% of species pairs sampled, based on a combined sample of ~361 species from South Africa and California (exact frequencies and sample sizes depended on the ecological character being analysed; [van der Niet and Johnson 2009](#), [Anacker and Strauss 2014](#)). Divergence typically involved habitat types and pollinators. There were numerous examples of ecological divergence between sister species of fungi, bacteria, and protists, but few quantitative analyses. However, host-switching represents ecological divergence, and this is frequently important in all three groups, especially protists and fungi ([Fig. 1](#)). The importance of ecological divergence is also supported by earlier synthetic studies (e.g. [Funk et al. 2006](#)).

An obvious caution here is that finding ecological divergence between sister species does not guarantee that this divergence caused their speciation. Nevertheless, it is a necessary line of evidence. Moreover, in some cases, there is additional evidence for the potential importance of these ecological traits for speciation, both from below and above the species level. For example, within many insect species there is evidence for genetic structure associated with different host plant species (review in [Forbes et al. 2017](#)). Above the species level, the presence of herbivory increases diversification rates ([Wiens et al. 2015](#)), and shifts to different clades of plant hosts increase diversification within herbivorous insect lineages ([Hardy and Otto 2014](#)). More broadly, there is an extensive literature relating speciation to herbivory in insects (e.g. [Ehrlich and Raven 1964](#), [Mitter et al. 1988](#), [Farrell 1998](#), [Mayhew 2007](#), [Futuyma and Agrawal 2009](#)).

A third generality was that prezygotic isolation may be more widespread and important than postzygotic isolation (see also [Coyne and Orr 2004](#)). In insects, 79% of 53 pairs had both pre- and postzygotic isolation, whereas 21% had only prezygotic, a potential signature of prezygotic isolation evolving first ([Coyne and Orr 1989, 1997](#)). In marine invertebrates, species are thought to generally be isolated by gametic incompatibility and temporal differences in spawning times, both forms of prezygotic isolation. In vertebrates, postzygotic isolation is thought to lag behind the evolution of distinct species, and viable hybrids can be produced between relatively ancient species (>20 Myr). In plants, prezygotic (i.e. prepollination) barriers

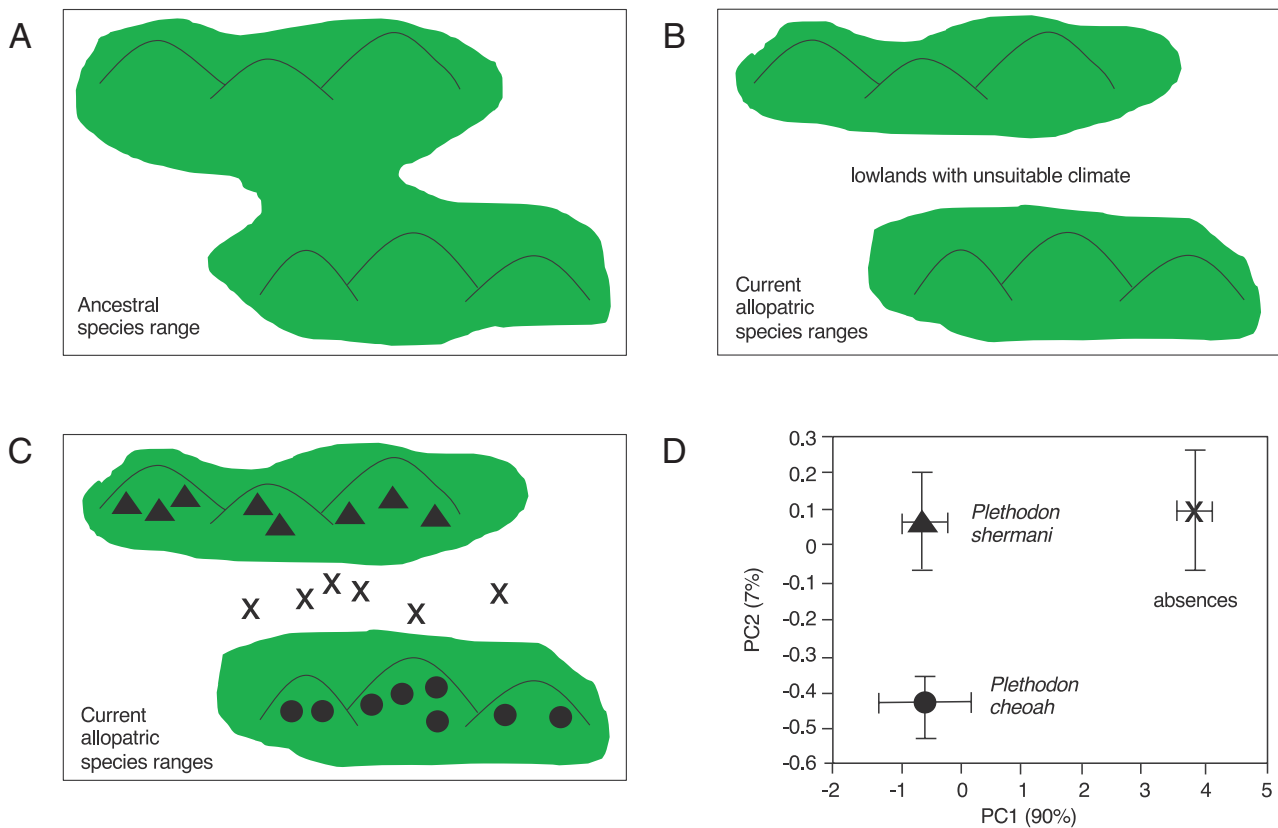
seem to contribute much more to overall reproductive isolation than postzygotic barriers ([Lowry et al. 2008](#), [Baack et al. 2015](#), [Christie et al. 2022](#)), but prezygotic barriers do not necessarily evolve first ([Widmer et al. 2009](#)). In fungi, the relationship between pre- and postzygotic isolation is not clear (e.g. [Le Gac and Giraud 2008](#)). Gametic incompatibility appears relatively frequent in protists, including 86% of 37 sister-species pairs considered by [Hernández-Hernández et al. \(2021\)](#). In bacteria, many species may be isolated by ecological divergence and an inability to recombine with individuals with more genetically divergent sequences ([Polz et al. 2013](#), [Cohan 2016](#)). These two factors may be analogous to prezygotic isolation. [Matute and Cooper \(2021\)](#) reviewed nine plant and animal (insects, fish) case studies and found that prezygotic isolation evolved more quickly than postzygotic isolation in three out of four animal case studies but not in the five plant studies.

### Do we know how allopatric speciation works?

In some ways, we know surprisingly little about the likely most common geographic mode of speciation: the allopatric mode. The classic model of allopatric speciation involves a ‘geographic barrier’ that splits a species into two sets of populations (incipient species). Many researchers might reasonably say that allopatric speciation is what happens next: the eventual evolution of intrinsic reproductive isolation between these geographically isolated populations. However, since this might not evolve for tens of millions of years, allopatric speciation might be considered to occur (or begin) when the species is split into two by the geographic barrier ([Wiens 2004a](#)).

Given this perspective, how does allopatry actually happen ([Fig. 3](#))? Based on first principles, a geographic barrier is not caused by a species’ adaptation to divergent ecological conditions: instead it is the failure to adapt to ecological conditions associated with the geographic barrier ([Wiens 2004b](#), [Hua and Wiens 2013](#)). A geographic barrier is not a giant, invisible wall that magically inserts itself between two sets of populations. Instead the barrier consists of ecological conditions that the ancestral species cannot occur in or disperse through. These unsuitable ecological conditions might include hotter lowland habitats for a montane, cool-adapted species, ocean for terrestrial species, or land for marine and freshwater species. The splitting involves not only unsuitable ecological conditions, but also the failure to adapt to those conditions over time (and maintain gene flow among the two sets of populations). After all, if the species could simply adapt to these conditions, then they would not form a barrier to dispersal and gene flow. Given this idea, a barrier to gene flow that splits an ancestral species into two arises through the failure of adaptation and ecological divergence, the opposite of the typical concept of ecological speciation (e.g. [Schluter 2001](#), [Rundle and Nosil 2005](#)).

This process can be called speciation through niche conservatism. Niche conservatism is the maintenance of one or more aspects of the ancestral ecological niche over time (e.g. [Peterson et al. 1999](#), [Wiens et al. 2010](#), [Crisp and Cook 2012](#)). Various population-level processes might underlie niche conservatism (and allopatry), including behavioural habitat selection, stabilizing selection on traits related to environmental tolerances, gene flow between populations preventing local



**Figure 3.** Allopatric speciation through niche conservatism. A, simplified example illustrating an ancestral species that occurs in two geographically separated mountain ranges. The range of the species is shown in green. During a period of cool climate, the ancestral species is able to occur in the lowlands between mountain ranges, maintaining gene flow between mountain ranges. B, after climate warms, the lowlands separating the two mountain ranges becomes uninhabitable for the species. Because the species is unable to adapt to these new ecological conditions (i.e. there is niche conservatism), the geographic range of the ancestral species is split into two sets of allopatric populations (ranges shown in green), which later are considered distinct allopatric species. C, hypothetical example showing sampling of localities in the geographic ranges of each species (triangles and circles) and the absence localities in between them (Xs; localities where the species was searched for but not found). D, empirical data from an allopatric sister-species pair of Appalachian salamanders that show climatic niche conservatism (from figure 4 of [Kozak and Wiens 2006](#)). The graph plots the first two axes of a principal component analysis (PCA) of the climatic variables. The circle and triangle show the mean values among localities for each species (lines indicate 95% confidence limits) whereas the X shows the mean value for the absence localities. If one only examines the climatic conditions where these two species occur, they appear to be distinct on PC2. However, PC2 describes only 7% of the climatic variation among localities. Most of the climatic variation (91%) is described by PC1, which differentiates the localities where these two species occur and the absence localities between their ranges. On PC1, the two species are almost indistinguishable. Allopatric speciation through niche conservatism is determined by the climatic differences between where species occur and where they do not occur. Considering only the climate where species occur may be misleading, but is done in many analyses relating climate and speciation. Note that in the study by [Kozak and Wiens \(2006\)](#), two other species pairs show very similar patterns to those shown here, whereas other pairs show more divergence on PC1.

adaptation to conditions at the range edges, competition with species in the unsuitable habitat, and trade-offs between traits that limit adaptation to novel conditions (reviews in [Wiens et al. 2010](#), [Crisp and Cook 2012](#), [Donoghue and Edwards 2014](#), [Pyron et al. 2015](#)).

The role of niche conservatism in speciation has been the subject of considerable research (and confusion). The field began with the classic paper by [Peterson et al. \(1999\)](#), who found evidence for climatic niche conservatism among sister species of Mexican animals using species-distribution modelling. Some subsequent studies supported this pattern (e.g. [Kozak and Wiens 2006](#)) whereas others found ecological divergence instead (e.g. [Graham et al. 2004](#)).

A fundamental problem in many studies is that they only compare the climatic niches of sister species, and do not address

whether there is a barrier of unsuitable habitat between them (thus largely missing the process by which niche conservatism would actually drive allopatry and allopatric speciation; [Fig. 3](#)). This issue applies to the widely used ENM approach for testing niche conservatism ([Warren et al. 2008, 2010](#)), to the recent analysis of allopatric speciation by [Anderson and Weir \(2022\)](#), to analyses of relationships between niche divergence and diversification among clades (e.g. [Kozak and Wiens 2010](#), [Cooney et al. 2016](#)), and to analyses of models of niche evolution on phylogenies (e.g. testing for Brownian motion vs. Ornstein–Uhlenbeck models). Sister species might appear to have divergent niches when considering only the climates where they occur, while having very similar niches when compared to the barrier of unsuitable habitat between them ([Fig. 3D](#)). Some conceptual papers do not seem to appreciate the importance of

a barrier of unsuitable habitat (Pyron *et al.* 2015). A review of niche conservatism in empirical studies (Peterson 2011) also did not address the climatic suitability of the region between the ranges of sister species (but nevertheless concluded that niche conservatism was prevalent among the species pairs examined). Importantly, allopatric sister species might have similar climatic niches or divergent ones, but if there was allopatric speciation through climatic niche conservatism, then there should be a region separating their geographic ranges that is climatically unsuitable for them, either now or (more importantly) during the inferred time frame of their split (Fig. 3).

That being said, testing for a barrier of unsuitable climate between two allopatric sister species can be complicated and frequently ambiguous (e.g. Hua and Wiens 2010, Jezkova and Wiens 2018). The simple expectation under niche conservatism is that the geographic range of each species will be climatically suitable for the other species based on species-distribution modelling, whereas the area between them (i.e. geographic barrier) will be unsuitable for both. However, many other outcomes are often observed, such as the intervening area being suitable for one species but not the other. Further, broader analyses often support niche divergence over conservatism. For example, among 49 sister-species pairs of squamates (lizards and snakes), 61–76% supported climatic-niche divergence (depending on the methods), and only ~20% were consistent with niche conservatism (Jezkova and Wiens 2018). Simple alternative explanations (e.g. increasing niche divergence between sister species over time) were not supported.

Furthermore, many studies have found higher rates of species diversification (speciation–extinction) associated with higher rates of climatic-niche evolution among clades (e.g. plants: Schnitzler *et al.* 2012; amphibians: Kozak and Wiens 2010, Moen and Wiens 2017; birds: Cooney *et al.* 2016; mammals: Castro Insua *et al.* 2018; squamate reptiles: Li and Wiens 2022). This pattern is more consistent with speciation through niche divergence than niche conservatism (although it does not rule out both occurring, depending on the species, or niche divergence after speciation through niche conservatism). Based on simulations, Qiao *et al.* (2024) concluded that lineages with niche conservatism have higher diversification rates than those with labile niches (in contrast to these empirical studies). However, the only speciation process simulated was allopatric speciation involving barriers of unsuitable climatic conditions. This assumption may have biased the results to favour speciation through niche conservatism.

Given that empirical results often do not support the model of allopatry through climatic niche conservatism, why are so many sister species allopatric? Species might be separated by ecological barriers unrelated to climate, such as an absence of rock outcrops for rock-dwelling species. In this case, niche conservatism could still be involved, but might involve conservatism in nonclimatic ecological variables (e.g. microhabitat). However, if nonclimatic factors were involved, there is no reason to expect the divergent climatic niches observed in allopatric sister species. One potential explanation (Jezkova and Wiens 2018) is that allopatry caused by nonclimatic factors (microhabitats, species interactions, stochastic dispersal, or extinction) might be more likely to lead to speciation if the allopatric populations are

climatically divergent, such that climatic and nonclimatic factors act synergistically to drive speciation between population pairs that might otherwise merge without speciating (ephemeral speciation; Rosenblum *et al.* 2012).

In summary, allopatric speciation has long been considered the most common geographic mode (Mayr 1963, Coyne and Orr 2004), but we still do not understand how it works. This is (in part) because we do not know how species become allopatric. An important agenda for future studies is to actually address this question, and not simply test whether sister species have similar climatic niches or not. Additional theoretical studies on the process of allopatric splitting would also be valuable.

### Majority and minority processes within groups

Life is diverse, and so is speciation. Although the focus here is on typical speciation, some speciation processes are uncommon but still potentially important.

One example is polyploidy. Polyploidy may underlie ~15% of speciation events in land plants (Wood *et al.* 2009). It is clearly not ‘typical’ but not trivial either. Polyploid speciation is also present but infrequent in protists, fungi, and some animals (Hernández-Hernández *et al.* 2021). For example, in protists it was potentially involved in speciation in 11% of 37 species pairs. Polyploidy is present but very uncommon in fungi and in many animals, including vertebrates, insects, crustaceans, and molluscs (Campbell *et al.* 2016).

Hybrid speciation is another example. Hybrid speciation has been hypothesized in plants, animals, and fungi (Hernández-Hernández *et al.* 2021). There has been debate about how hybrid speciation should be defined, and by association, how common it is (Schumer *et al.* 2014, Feliner *et al.* 2017). However, no one has suggested that hybrid speciation accounts for most speciation in any group. Instead, there is disagreement about whether there are only about four well-supported examples (Schumer *et al.* 2014) or >30 (Feliner *et al.* 2017).

The same may apply to sympatric speciation. In each major group, only a minority of sister-species pairs are even candidates for sympatric speciation (i.e. fully sympatric), but they nevertheless make up a nontrivial percentage of species pairs (10–26%; Hernández-Hernández *et al.* 2021).

In summary, these three widespread speciation processes seem unlikely to be the most common in any group. Nevertheless, these ‘minority processes’ might together drive much of the speciation in many groups across life.

### Speciation in cryptic insect species

We cannot determine what speciation processes drive the origin of most species without knowing what most species are. For example, if most species are host-associated, then typical speciation may be some combination of host-switching and co-speciation.

Along these lines, another factor that may determine the diversity of life is the number of cryptic species (i.e. undescribed species detected based on nonmorphological data within a species initially delimited from morphological data; Bickford *et al.* 2007). For example, recent analyses (Li and Wiens 2023) suggest that the typical morphology-based insect species might conceal about three cryptic species on average. This analysis considered many potential factors that might influence this number,

such as variation among insect orders, sample sizes within species, nuclear vs. mitochondrial markers, tropical vs. temperate occurrence, different species-delimitation methods, and biased species sampling. The overall estimate of about three cryptic species per morphology-based species was robust to these sources of variation and bias. Insects make up roughly half of all described species, and many independent estimates suggest that there are ~5 million additional undescribed insect species, based on morphological criteria (review in [Stork 2018](#)). Given this, the factors driving speciation among cryptic insects might be among the most frequent factors driving speciation across life.

What do we know about speciation in cryptic insect species? There have been few synthetic studies, despite older reviews on host races (i.e. genetically divergent individuals associated with different host-plant species; [Dres and Mallet 2002](#)) and on cryptic orthopterans (e.g. crickets) detected via acoustic signals ([Walker 1964](#)).

Here I performed a brief review of cryptic speciation in insects. I searched Google Scholar on 4 June 2024 using the keywords ‘insects cryptic species speciation’ (but not in quotes). I found 32 000 results and sorted them by relevance. I examined the first 100. By the last sets of 10, relatively few were relevant. Nevertheless, these results should be considered a sample of the literature and not an exhaustive review.

The 50 usable studies are summarized in [Supporting Information Dataset S1](#) (i.e. excluding review papers, studies that only delimited cryptic species, and those that failed to find them). Most studies were in the most species-rich orders (Coleoptera = 6; Diptera = 13; Hemiptera = 6; Hymenoptera = 13; Lepidoptera = 8) with single studies on smaller orders (Dermaptera, Ephemeroptera, Neuroptera, Plecoptera). These studies should broadly represent insect diversity. The majority used both nuclear and mitochondrial sequence data to identify cryptic species ( $N = 27$ ), some used only mitochondrial data ( $N = 12$ ; but often with other evidence), and others used different types of nuclear data (allozymes, microsatellites, RADseq;  $N = 7$ ). The remainder ( $N = 4$ ) studied cryptic species delimited in earlier studies.

Surprisingly, cryptic species were not predominantly allopatric (in contrast to morphology-based species pairs). Relative to their close relatives, cryptic species were sympatric or mostly sympatric ( $N = 17$  studies), and less often allopatric or mostly allopatric ( $N = 12$  studies). Several studies contained multiple cryptic species that had a mixture of allopatric and sympatric distributions ( $N = 7$ ). In other studies species were partly sympatric ( $N = 4$ ), parapatric or mostly parapatric ( $N = 4$ ), allopatric or parapatric ( $N = 2$ ), or with unclear distributions ( $N = 4$ ). More research will be needed to determine if the surprising prevalence of sympatric cryptic species arises from sympatric speciation or from secondary contact after allopatric origins.

Cryptic species were associated with divergent host usage in 24% ( $N = 12$ ) of these studies. These hosts were mostly plants ( $N = 9$ ; 75%), but also included flies and aphids (for parasitoid wasps;  $N = 2$ ) and ants (for myrmecophilous flies;  $N = 1$ ). Many insects are not herbivorous, and some herbivores had cryptic species that were not host-associated. Among the remaining studies, the potential barriers underlying reproductive isolation were often unclear ( $N = 14$ ), but hypothesized barriers

included large-scale climatic-niche divergence ( $N = 5$ ), temporal partitioning of mating ( $N = 2$ ), habitat differences within broad-scale sympatry, including nesting sites ( $N = 3$ ), mate choice ( $N = 3$ ), differences in song ( $N = 1$ ; for lacewings), and postzygotic isolation ( $N = 2$ ; low hybrid fitness). Across all studies, there were three in which isolation may have involved karyotypic divergence (e.g. chromosome number), four involving temporal isolation (i.e. mating at nonoverlapping times of the year), and two possibly involving the bacteria *Wolbachia*.

In summary, uncovering speciation processes in cryptic insect species may be an important area for future research. Some factors are important for both cryptic and morphology-based species (e.g. host-associated speciation) whereas other aspects are more surprising and uncertain (e.g. the prevalence of sympatry among cryptic species).

## SPECIATION AND THE ORIGINS OF RICHNESS PATTERNS

### Overview

A major goal of evolutionary biology and ecology is to understand how patterns of species richness arise. These richness patterns include spatial patterns (like the latitudinal diversity gradient), patterns among clades (like the dominance of angiosperms among plants), and trait-based patterns (like the preponderance of species with sexual reproduction vs. asexual reproduction, the ‘paradox of sex’).

These richness patterns must ultimately be explained by speciation, because speciation is the ultimate source of all species. However, they are not necessarily explained by variation in rates of speciation. Instead, they might be explained by the balance of speciation and extinction over time (i.e. net diversification rates, diversification rates hereafter) and by the relative time available for speciation, including the time since the origin of a clade, the time of colonization of a region, or when a given character state evolved. Studying macroevolutionary patterns of speciation and diversification from phylogenies can provide insights into the causes of these richness patterns. Conversely, such macroevolutionary analyses can provide insights into the factors that promote speciation (e.g. particular traits associated with high diversification rates).

In this section, I will do two main things. First, I will review (some) methods that are available to estimate rates of speciation and diversification, and how they can be used to elucidate the causes of richness patterns and drivers of speciation. In doing so, I will address some potential misconceptions about which methods are useful for elucidating the origins of biodiversity patterns. Second, I will briefly review what has been learned about the origins of richness patterns from macroevolutionary studies, and what these studies tell us about speciation.

### Estimating diversification and speciation rates from phylogenies

A plethora of methods have been used to estimate rates of speciation, extinction, and diversification. Strong claims have been made about which methods are useful for understanding richness patterns and which are not (e.g. [Rabosky and Benson 2021](#)). Here, I will address these claims and briefly review some widely

used methods. These methods can be classified based on what units the rates are being estimated for. These include methods that estimate rates for individual species, for entire clades, and for specific character states. These methods generally utilize time-calibrated molecular phylogenies for living species to estimate rates.

#### *Species-based estimators*

Several methods can be used to estimate rates for individual species from time-calibrated species-level phylogenies (Morlon *et al.* 2024). These species-level rates can then be related to specific traits (e.g. latitudinal distribution) using phylogenetic comparative methods. One widely used species-level estimator is the DR (diversification-rate) statistic (Jetz *et al.* 2012). This not a model-based method, but is readily calculated for each species in a tree. BAMM (Bayesian Analysis of Macroevolutionary Mixtures; Rabosky 2014) is another frequently used method, which identifies a limited number of large shifts in diversification rates on phylogenies, and assigns estimated rates to each species. ClaDS (cladogenetic diversification rate shift; Maliet *et al.* 2019, Maliet and Morlon 2022) is a Bayesian method that estimates rates for each branch and allows for many small changes in rates, rather than the few large changes assumed by BAMM. The new likelihood method MiSSE (Vasconcelos *et al.* 2022) can also estimate relatively small changes in rates across trees.

Maliet *et al.* (2019) found that ClaDS often outperformed BAMM and the DR statistic. For example, using simulations (their fig. S24) they found that BAMM yielded relatively weak correlations between true and estimated rates among species when rates changed continuously across the tree ( $r \sim .2$ ,  $r \sim .4$ , and  $r \sim .6$  for trees with 50, 100, and 200 tips), whereas ClaDS performed better ( $r \sim .6$ ,  $r \sim .8$ , and  $r \sim .8$ ). The performance of the DR statistic was intermediate ( $r \sim .5$ – $.6$ ). When simulated conditions were more favourable for BAMM, with a few large shifts in diversification rates (their fig. S23), BAMM and ClaDS performed similarly (for both methods  $r \sim 0$  for 50 tips and  $r \sim .9$  for 100 tips; for 200 tips  $r \sim .9$  for BAMM and  $r \sim .8$  for ClaDS), and the DR statistic generally performed more poorly (for 50, 100, and 200 tips,  $r \sim .1$ ,  $r \sim .5$ , and  $r \sim .6$ ).

Vasconcelos *et al.* (2022) compared the relative performance of MiSSE, BAMM, ClaDS, and the DR statistic (among other methods) in simulations using absolute mean error (deviation between estimated and true rates for each species) rather than correlations. They found that the relative performance of MiSSE, BAMM, and ClaDS varied across simulated conditions and diversification variables (speciation, extinction, diversification, etc.). MiSSE generally performed well across diverse conditions, but the DR statistic did not. ClaDS performed poorly when there was no rate variation among branches, whereas BAMM performed poorly when rates varied continuously.

Several other simulation studies found that BAMM is insensitive to variation in diversification rates across phylogenies (e.g. Moore *et al.* 2016, Kodandaramiah and Murali 2018, Meyer and Wiens 2018, Meyer *et al.* 2018). For example, BAMM can incorrectly assign high diversification rates to smaller clades in which true rates are low (Meyer and Wiens 2018). However, this problem may be masked in simulations in which large clades have their rates estimated accurately, small clades have

their rates estimated poorly, and each tip is counted separately when assessing accuracy, such that the overall results are dominated by the many tips from the larger clade (which are not independent). This problem applies to the two studies mentioned above (Maliet *et al.* 2019, Vasconcelos *et al.* 2022), and others (e.g. Title and Rabosky 2019).

The problem of insensitivity to rate variation can also be seen in empirical datasets. For example, within a given clade (e.g. a family) BAMM can estimate one rate for a genus when the whole family is analysed, but a very different rate when that same genus is analysed alone. Alarming, there is often no significant correlation between these two sets of estimated rates (based on analyses in snakes, tortoises, and birds: Meyer and Wiens 2018, Meyer *et al.* 2018). Rabosky (2019) suggested that these comparisons are inappropriate because they are based on correlations from point estimates of diversification rates. However, similar point estimates and correlations were used in simulations to argue for BAMM's accuracy (e.g. Rabosky 2014, Title and Rabosky 2019). Furthermore, these alarming differences occur even when individual clades (e.g. genera, families) have many species (Meyer *et al.* 2018). Comparisons across snake clades suggest that BAMM estimates from clades in isolation are significantly correlated with estimates from other methods, whereas estimates from BAMM from across the tree are inconsistent with other methods (Table 1). Thus, forcing BAMM to estimate rates for clades in isolation prevents BAMM from assigning the same rate to different clades with very different rates. Simulations show that estimating rates for clades in isolation dramatically increases the accuracy of BAMM (Meyer and Wiens 2018). However, this is not how BAMM is generally used. Although smaller clades may have their rates estimated less accurately in isolation than larger clades (Meyer *et al.* 2018), it is unclear at what point the disadvantages of analysing smaller clades in isolation becomes worse than BAMM's tendency to assign the same rate to clades with different true rates (but using clades of 10 or more species increased accuracy; Meyer and Wiens 2018). In summary, if one is interested in the variation in speciation and diversification rates across a phylogeny, then a method that is insensitive to that variation may be problematic.

This is not a comprehensive review of species-based estimators. Instead, I highlight newer methods that appear promising (ClaDS, MiSSE) and older methods that seem problematic (BAMM, DR statistic). Methods that are consistently accurate across diversification scenarios are still needed. As new methods are developed it is essential that they be thoroughly compared to existing methods (e.g. Maliet *et al.* 2019, Vasconcelos *et al.* 2022). It is also important to evaluate how methods perform given limited taxon sampling, since phylogenies rarely contain all known species within a clade.

#### *Clade-based estimators*

Another class of methods estimates diversification rates for entire clades. Many of these use time-calibrated, species-level phylogenies within a clade to estimate that clade's speciation, extinction, and net diversification rates (e.g. Nee *et al.* 1994; MEDUSA: Alfaro *et al.* 2009; RPANDA: Morlon *et al.* 2011, 2016; Silvestro *et al.* 2011, Stadler 2011, Etienne *et al.* 2012; reviews in Morlon 2014, Morlon *et al.* 2024). Other methods use



**Table 1.** Comparison of estimated diversification rates among 15 snake clades using four different approaches for estimating rates.

Methods compared	$r^2$	P-value
BAMM whole tree vs. BAMM clades	.235	.0667
<i>diversitree</i> vs. MS estimator	.695	<b>.0001</b>
<i>diversitree</i> vs. BAMM clades	.829	<b>&lt;.0001</b>
<i>diversitree</i> vs. BAMM whole tree	.220	.0780
MS estimator vs. BAMM clades	.754	<b>&lt;.0001</b>
MS estimator vs. BAMM whole tree	.182	.1130

Results are from standard linear regression among clades. BAMM was applied to the entire snake phylogeny (BAMM whole tree) or to each of the 15 separate clades (BAMM clade). When BAMM was applied across the tree (BAMM whole tree), as usually done, then the estimates from BAMM are only weakly related to estimates from other methods (and to the other rates from BAMM). Otherwise, the rates estimated by different methods are strongly related to each other. Significant results are in bold. The R package *diversitree* (FitzJohn 2012) was used to estimate diversification rates using the approach of Nee *et al.* (1994). The MS estimator used stem-group ages of clades and  $\epsilon = .5$ . The table is taken from Li and Wiens (2022).

only the age of the clade and its species richness to estimate the diversification rate (e.g. method-of-moments estimator, MS estimator hereafter: Magallón and Sanderson 2001). Although the MS estimator is not designed to estimate separate speciation and extinction rates, it is advantageous in being relatively insensitive to incomplete species sampling, especially the stem-based estimator (Meyer and Wiens 2018). Incomplete sampling is potentially problematic for other species- and clade-based estimators (e.g. BAMM; Meyer and Wiens 2018). There is also controversy about whether speciation and extinction rates can be accurately disentangled, with some authors suggesting that they cannot (Louca and Pennell 2020) and others suggesting that they can (Helmstetter *et al.* 2022, Morlon *et al.* 2022, Kopperud *et al.* 2023).

Some authors have concluded that the MS estimator cannot resolve the causes of biodiversity patterns (Rabosky and Benson 2021). The primary evidence used to support this claim was an analysis of species richness over time in the fossil record, which showed that diversification rates estimated from richness in the past did not always predict future species richness (e.g. the method did not predict the effects of mass extinctions and key innovations that had not yet happened). This is not what the method is used for. Moreover, Rabosky and Benson (2021) only analysed the MS estimator, rather than comparing it to other methods. Therefore, it might actually be the best method according to this criterion (i.e. had they included other methods), the opposite of their conclusions. They also suggested that separate speciation and extinction rates were not identifiable from this method. However, again this method is not designed to estimate separate speciation and extinction rates. Finally, they suggested that the rate estimates from the MS estimator depend on clade age: they depend on both clade ages and species richness (Magallón and Sanderson 2001).

The standard approach to address the accuracy of a method for estimating diversification rates is to test how well it estimates known rates in simulations. This was not done by Rabosky and Benson (2021). Simulations suggest that the MS estimator yields strong relationships between true and estimated rates, including when rates are constant within clades but variable among clades, when rates are variable among subclades within a clade but constant within subclades over time, and when clades are variable over time within clades, including linear and exponential increases and decreases in both speciation and extinction

rates over time (Kozak and Wiens 2016, Meyer and Wiens 2018, Meyer *et al.* 2018). For example, using the crown-group MS estimator with the standard correction for extinct clades ( $\epsilon = .5$ ) and full species sampling (Meyer *et al.* 2018), the relationship between true and estimated diversification rates gives  $r^2 = .70$  when rates are constant within clades but variable among clades,  $r^2 = .67$  when rates vary between subclades within each clade, and  $r^2 = .71$  when speciation and extinction rates vary over time within each clade. Some authors (e.g. Rabosky and Benson 2021) claimed that the MS estimator requires constant rates, but the relationships between true and estimated rates were strong regardless of whether rates were constant or variable among and within clades. Furthermore, recent empirical analyses suggest that net diversification rates for individual clades estimated from the MS estimator are strongly correlated with those from ClaDS (Yu and Wiens 2024) and other methods (Table 1). Given these results, the idea that the MS estimator is uniquely unable to resolve the drivers of biodiversity patterns seems very strange indeed (see also next section, describing empirical studies that used the MS estimator to resolve the drivers of biodiversity patterns).

Indeed, simulations suggest that the MS estimator can be more accurate than BAMM. For example, when BAMM is applied to the same simulated trees with full sampling and constant rates within clades but variable rates among clades (and analysing the entire tree), the relationship between true and estimated rates among these clades yields only  $r^2 = .37$  whereas the MS crown-group estimator yields  $r^2 = .70$  (Meyer and Wiens 2018). Again the accuracy of the MS estimator was almost identical when rates were constant vs. variable within clades (see above).

Given a set of estimated rates for a set of clades, one can use phylogenetic regression (Martins and Hansen 1997) and related approaches to test relationships between traits and diversification rates. This overall approach is especially useful because it is relatively straightforward to include multiple traits and estimate how much variance in diversification rates is explained by each one.

However, this approach can have disadvantages also. First, the MS estimator does not estimate separate speciation and extinction rates. A ratio of speciation to extinction rates ( $\epsilon$ ) is assumed to correct for clades that are unsampled due to extinction (Magallón and Sanderson 2001). Different values of  $\epsilon$  give different estimated diversification rates, but different  $\epsilon$  values generally have limited impact in empirical studies testing the

correlates of diversification (e.g. [Chen and Wiens 2021](#)) and simulation studies examining their accuracy (e.g. [Meyer and Wiens 2018](#)). Second, this approach requires estimating rates for selected clades. These might be named higher taxa (e.g. phyla), or based on clade ages instead. These clades may not perfectly match the distribution of traits or of changes in diversification rates. Thus, the raw data may be the frequency of a trait within a clade, making the linkage between traits and rates less direct. Furthermore, results can be sensitive to how the group is subdivided into clades (but conclusions need not be overturned; [Jezkova and Wiens 2017](#)). Third, estimating rates for clades with a single species is challenging (and many higher taxa have only a single living species). For the stem-group estimator, the estimated rate will be zero (it cannot be estimated for the crown-group estimator, since single-species clades lack a crown group). A rate of zero can accurately reflect that the single-species clade has a relatively low net diversification rate if the clade is old, but a rate of zero for a young, single-species clade is misleading. Caution is needed in these cases.

This discussion has focused on rates from phylogenies. It is possible to estimate diversification, speciation, and extinction rates of clades using Bayesian fossil-based methods (PyRate; [Silvestro et al. 2014a, b](#)). However, morphological data may greatly underestimate species numbers in living taxa (e.g. cryptic insect species), and this problem will be exacerbated with the incomplete and fragmentary morphological information from fossils.

Finally, species-level estimators can also be used to estimate overall speciation and diversification rates for higher-level clades (e.g. BAMM, ClaDS; see above). However, these may require relatively complete, time-calibrated, species-level phylogenies within clades. Such phylogenies are unavailable for many groups.

#### *Trait-based estimators*

Instead of estimating rates for species or clades, an alternative approach is to estimate diversification rates for each character state of a given character (trait). For example, for the character diet the states may be herbivory, omnivory, and carnivory. SSE models (state-dependent speciation and extinction) have become widely used for testing hypotheses about how traits are related to diversification. These include methods for binary (two-state) discrete variables (BiSSE; [Maddison et al. 2007](#)), multistate discrete variables (MuSSE; [FitzJohn 2012](#)), quantitative traits (QuaSSE; [FitzJohn 2010](#)), and multiple states and traits (secSSE; [Herrera-Alsina et al. 2019](#)). These methods estimate speciation and extinction rates associated with each state.

[Rabosky and Goldberg \(2015\)](#) concluded that SSE models have high rates of type-1 error (i.e. falsely rejecting the null hypothesis of equal rates). Specifically, they found that when they simulated the evolution of a trait on empirical trees and analysed the data with BiSSE, a model of trait-dependent diversification was often chosen over a null model. However, [Beaulieu and O'Meara \(2016\)](#) pointed out that the null model in these analyses was inappropriate, because the empirical trees were presumably not generated under the null model of constant speciation and extinction rates (e.g. in cetaceans) and the simulated traits clearly did not influence the speciation and extinction rates that generated these trees. Therefore, BiSSE was being forced to choose between two incorrect models (i.e. constant speciation

and extinction across the tree vs. variable speciation and extinction rates related to the simulated trait). This makes the selection of an incorrect model inevitable. [Beaulieu and O'Meara \(2016\)](#) developed an approach which allowed a more appropriate null model to be chosen, in which speciation and extinction rates vary but are related to a 'hidden' trait different from the focal, observed trait (HiSSE; also secSSE).

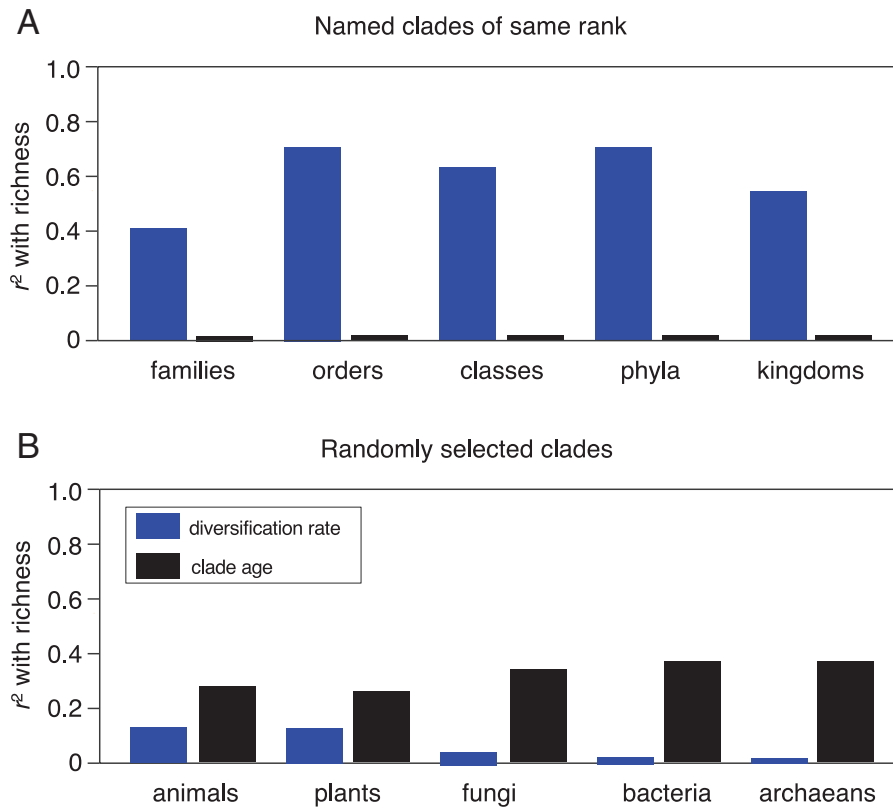
HiSSE models have now become widely used. However, they (and other SSE methods) do present some challenges. First, they estimate overall speciation and extinction rates associated with each trait, and do not necessarily include variation in those rates among species across the tree. Similarly, as noted by [Beaulieu and O'Meara \(2016\)](#) and previous authors (e.g. [Maddison and FitzJohn 2014](#)), the method does not correct for phylogenetic nonindependence of species, such that the association between rates and traits could be based on a single trait origin. A statistical association between multiple origins of a character state and parallel increases in speciation or diversification rates would provide stronger evidence that the state increased diversification. Attempts to statistically test HiSSE rates across trees have been controversial (e.g. [Moen 2022](#)). Second, this approach does not address how much variation in diversification rates across the tree is explained by the observed trait. Thus, a trait associated with variation in diversification rates might explain 95% of that variation or less than 5%. These problems might be solved by using MiSSE to estimate rates for each species and linking rates and traits among species statistically. Third, simulations show that SSE trait-based methods can give problematic results when one state is rare (present in <10% of species) and/or when <300 species are sampled ([Davis et al. 2013](#)). Fourth, these methods are sensitive to incomplete species sampling (<60%) and to uneven sampling among clades ([Mynard et al. 2023](#)).

## What explains patterns of species richness?

### *Overview*

Here I will address the causes of three main types of species richness patterns: clade-based, spatial, and trait-based. I will show that clade-based patterns among taxa of the same rank are generally explained by differences in diversification rates. These differences in diversification rates are then related to traits, especially ecological variables. However, spatial richness patterns (e.g. latitudinal diversity gradient) are more often explained by when each location (e.g. region, habitat) was successfully colonized, such that richness is explained by the time available for speciation not the rate of speciation. The same applies to trait-based richness patterns (e.g. number of species with each character state): richness is more often explained by when each state evolved, not the diversification rates associated with each state.

Note that I generally focus here on diversification rates rather than speciation rates. Some of the methods used (e.g. MS estimator) estimate net diversification rates and do not disentangle the relative contributions of speciation and extinction rates. Further, if a richness pattern is unrelated to diversification rates, it seems unlikely that it will be explained by speciation rates instead.



**Figure 4.** The drivers of richness patterns among clades, based on  $r^2$  between species richness and diversification rates (blue) and species richness and clade age (black). **A**, in comparisons of clades of the same taxonomic rank (e.g. families, phyla) across living organisms, there are strong positive relationships between species richness of clades and their diversification rates. The relationships between richness and clade age are either nonsignificant with very low  $r^2$  (effectively 0; families, orders), or are significant but negative (classes, phyla, kingdoms; older clades have lower richness). For simplicity, these are all shown as  $r^2$  of 0. Results are from phylogenetic regression analyses in [Scholl and Wiens \(2016\)](#) using the stem-group MS estimator. Sample sizes for each comparison are as follows: families ( $N = 2558$ ), orders ( $N = 434$ ), classes ( $N = 122$ ), phyla ( $N = 71$ ), and kingdoms ( $N = 8$ ). **B**, in comparisons of randomly selected clades within major groups across life, the species richness of clades is more strongly related to their ages than to their diversification rates. Results are from phylogenetic regression analyses in [Yu and Wiens \(2024\)](#) using the crown-group MS estimator. Sample sizes of clades within each group are as follows: animals ( $N = 496$ ), plants ( $N = 485$ ), fungi ( $N = 476$ ), bacteria ( $N = 434$ ), and archaeans ( $N = 440$ ).

#### Clade-based patterns

Some of the most dramatic biodiversity patterns involve the relative richness of clades of the same taxonomic rank. For example, ~90% of land plant species belong to the phylum Magnoliophyta (i.e. angiosperms, flowering plants) and not the other nine phyla, whereas ~80% of animal species belong to the phylum Arthropoda, and not the ~33 other animal phyla ([Bánki et al. 2024](#)). What explains these (and other) differences in richness among clades? Two hypotheses ([McPeck and Brown 2007](#)) are that these patterns are related to either clade ages (older clades had more time to accumulate species) or diversification rates (species accumulate more quickly).

Large-scale analyses ([Fig. 4A](#)) suggest that these differences in richness among clades of the same taxonomic rank (e.g. phyla, families) are generally explained by differences in net diversification rates, and not clade ages ([Scholl and Wiens 2016](#)). Diversification rates explain considerable variation in species richness among kingdoms ( $r^2 = .55$ ), phyla ( $r^2 = .72$ ), classes ( $r^2 = .64$ ), orders ( $r^2 = .72$ ), and families ( $r^2 = .41$ ) across life. Results were generally similar within animals, plants, fungi, protists (SAR clade), bacteria, and archaeans. Other studies have also found strong relationships between richness and diversification rates, such as among insect orders ( $r^2 = .62-.89$ ; [Wiens et al. 2015](#)), major vertebrate clades

( $r^2 = .80-.88$ ; [Wiens 2015a](#)), and land plant phyla ( $r^2 = .80-.92$ ; [Hernández-Hernández and Wiens 2020](#)).

Some readers might be concerned that such results are circular, because richness is used to calculate diversification rates. However, a relationship between diversification rates and richness is not inevitable. These strong relationships were not universal (e.g. absent among phyla of the SAR clade), and are weakest when there is a strong positive relationship between clade age and richness or a strong negative relationship between clade age and diversification rates ([Scholl and Wiens 2016](#)). Further, when clades are chosen randomly (see below), strong relationships between diversification rates and richness are often absent ([Fig. 4B](#); [Yu and Wiens 2024](#)). Finally, under a standard definition of circularity, the methods would predetermine the results and the results would then determine the choice of method. Clearly that scenario does not apply here.

Other studies have not always found strong relationships between diversification rates and richness. [Rabosky et al. \(2012\)](#) and [Hedges et al. \(2015\)](#) concluded that diversification rates did not determine richness patterns among clades, but did not directly test this hypothesis. [McPeck and Brown \(2007\)](#) found that richness patterns were generally explained by clade ages and not

diversification rates, but most of their results were from relatively young, species-poor clades.

Overall, richness patterns among clades of the same rank are generally explained by their diversification rates, at least among families and older clades. However, if clades are chosen randomly (but avoiding overlap between clades), then clade ages are generally more important than diversification rates for explaining species richness, based on an analysis across life (Fig. 4B; Yu and Wiens 2024). Among these randomly selected clades, the effect of clade age is stronger and the effect of diversification rates is weaker (Fig. 4). Most randomly selected clades are relatively young and have few species (as are most living clades), and these would need to have extremely high diversification rates to overcome the effects of clade age.

#### *What drives diversification and speciation?*

Given that many patterns of clade-based richness are explained by diversification rates, what then explains variation in diversification rates? The short answer may be traits. Many studies have identified traits that seem to underlie much variation in diversification rates among clades, using clade-based approaches. Examples from our work include insect pollination among plant phyla (Hernández-Hernández and Wiens 2020), herbivory among insect orders (Wiens *et al.* 2015), and terrestrial habitat use among plant phyla (Román-Palacios *et al.* 2022), animal phyla (Wiens 2015b, Jezkova and Wiens 2017), and major vertebrate clades (Wiens 2015a). The variance in diversification rates explained by these traits in each study ranged from ~30% to ~67%. On the other hand, range size and rates of climatic-niche evolution may be more important at smaller phylogenetic scales, including in analyses among families of land plants (Hernández-Hernández and Wiens 2020), fish (Tedescos *et al.* 2017), frogs (Moen and Wiens 2017), lizards and snakes (Li and Wiens 2022), birds (Cooney *et al.* 2016), and mammals (Castro-Insua *et al.* 2018). These results contradict the idea that the MS estimator cannot resolve the drivers of biodiversity patterns (Rabosky and Benson 2021).

Other studies have used SSE methods to identify traits that are related to increased diversification. The traits include nonfossorial habitat use in snakes (Cyriac and Kodandaramaiah 2018), diurnal diel activity in tetrapods (Anderson and Wiens 2017), freshwater habitat use in diatoms (Nakov *et al.* 2019), and traits related to pollination in plants, including hummingbird pollination in Gesneriaceae (Serrano-Serrano *et al.* 2017), nonhummingbird pollination in *Penstemon* (Wessinger *et al.* 2019), nectar spurs in Plantaginaceae (Fernandez-Mazuecos *et al.* 2019), and flower colour in Polemoniaceae (Landis *et al.* 2018). Note that all these studies used HiSSE.

A long-standing idea in ecology is that species interactions and local-scale ecology are important for diversity patterns over short timescales whereas large-scale geographic factors are more important over longer timescales (e.g. Ricklefs 1987). Although this idea was not originally applied to traits and diversification rates, the results described above suggest the opposite pattern. Specifically, traits related to species interactions seem especially important at deep timescales (among land plants and insects), along with local-scale habitat (terrestrial vs. aquatic or marine; among animal phyla, plants, and major vertebrate clades). By

contrast, traits related to range size and climatic niche seem especially important at shorter timescales (among families of plants and vertebrates). Of course, there are exceptions. Across life, multicellularity and sexual reproduction seem especially important (Chen and Wiens 2021). Microhabitat can still be important at smaller phylogenetic scales (e.g. among frog families; Moen and Wiens 2017), as can traits related to pollination (species interactions) within plant families (e.g. Serrano-Serrano *et al.* 2017, Fernandez-Mazuecos *et al.* 2019, Wessinger *et al.* 2019). This generalization was previously discussed (Wiens 2017) and was tested and supported in land plants (Hernández-Hernández and Wiens 2020).

What might explain this generalization? One potential explanation is that traits related to local-scale ecology (alpha niche) are more strongly conserved over macroevolutionary timescales and can apply to the deepest clades, whereas traits related to geography (beta niche) are less conserved and more variable among closely related lineages (e.g. Ackerly *et al.* 2006, Saban *et al.* 2023).

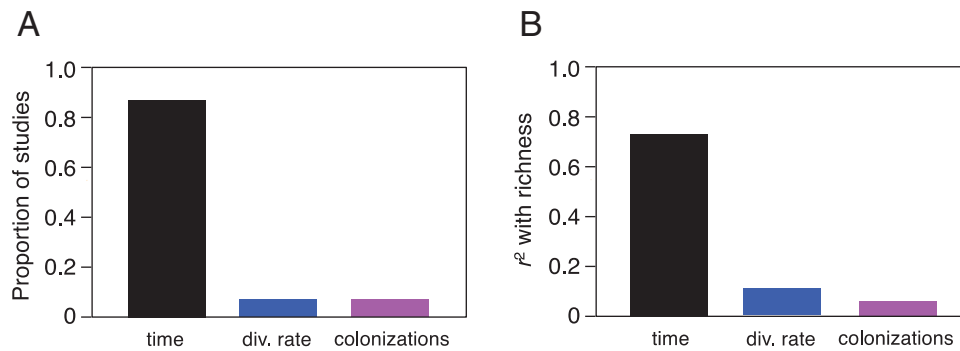
The linkages between these ecological variables and speciation seem clear in some cases, but less so in others. There is a large literature relating speciation to herbivory in insects (e.g. Ehrlich and Raven 1964, Mitter *et al.* 1988, Farrell 1998, Forbes *et al.* 2017), and speciation to pollination in plants (e.g. Grant 1949, Sargent 2004, van der Niet *et al.* 2014), including studies above and below the species level. There is also evidence for the role of climatic-niche divergence in speciation among species pairs (e.g. Graham *et al.* 2004, Jezkova and Wiens 2018). Marine habitat may lead to extensive dispersal, large geographic range sizes, and limited opportunities for allopatric speciation within species (May 1994, Vermeij and Grosberg 2010, Wiens 2015b, Tedescos *et al.* 2017), but further tests of these ideas are needed.

Interestingly, traits that are surprisingly difficult to link to speciation are those traits related to sexual selection (e.g. reviews in Kraaijeveld *et al.* 2011, Tsuji and Fukami 2020). For example, our recent analyses found no consistent effects of sexually selected traits on diversification across animals (Tuschhoff and Wiens 2023), sexually selected weapons in insects (Emberts and Wiens 2021), or sexual dichromatism in ray-finned fish (Miller *et al.* 2021). This is surprising because there is evidence for sexual selection underlying reproductive isolation among closely related species (e.g. Hoskin *et al.* 2005, Boul *et al.* 2007, Uy *et al.* 2018).

Of course many other traits may be important for speciation, diversification, and richness. I have tried to generalize based on analyses at broad scales, including analyses across animals and plants, and in some of the largest plant clades (angiosperms) and animal clades (insects, vertebrates).

#### *Geographic patterns of species richness*

Many studies have discussed the relationship between speciation rates and latitude as a way to understand the origins of higher richness in tropical regions relative to temperate regions (e.g. reviews in Mittelbach *et al.* 2007, Fine 2015, Schluter and Pennell 2017, Saupe 2023). However, the latitudinal diversity gradient is just one of many spatial richness patterns. Others include richness along gradients in elevation and climate and among habitats (e.g. marine, terrestrial, freshwater).



**Figure 5.** The drivers of richness patterns among geographic regions. A, in an analysis of 15 studies of plants and animals (Li and Wiens 2019), the variable most strongly related to richness patterns among regions in each study was identified (highest  $r^2$ ), and the proportion of studies in which each variable was the strongest predictor is shown. Patterns of species richness among regions were generally most strongly related to when each region was colonized (time, black bar) and not to variation in diversification rates among regions (div. rate, blue bar) or to the number of times each region was colonized (colonizations, purple bar). Two measures of colonization time are summed here, the estimated age of the first colonization of each region ( $N = 8$  studies) and the summed ages of all colonizations of each region ( $N = 5$  studies). B, the proportion of variance in species richness among regions explained by each variable (time, diversification rates, number of colonizations), averaged across the 15 studies (Li and Wiens 2019). For most studies ( $N = 10$ ) only time was significantly related to richness, but for five other studies the  $r^2$  for other variables was used. Variables that were not significantly related to richness were given a value of 0 when calculating the means across all studies.

All spatial richness patterns are directly determined by speciation, extinction, and dispersal (Ricklefs 1987). Given this, there are three direct explanations for geographic richness patterns. Certain regions have greater richness because: (i) of faster diversification rates among species that occur there, through higher speciation rates, lower extinction rates, or both; (ii) they were successfully colonized earlier than other regions, allowing more time for speciation to build up richness there—by ‘successful colonization’, I mean a colonization that persisted to the present, and thus contributes to modern species richness; and (iii) there were larger numbers of successful colonizations there. Various ecological factors might impact these diversification and dispersal rates, and the timing of colonization. Climate is an obvious candidate for explaining higher tropical richness, as is carrying capacity. However, these factors can only impact richness by influencing dispersal and diversification.

Many studies have now tested whether geographic variation in species richness is related to geographic variation in speciation or diversification rates. The results have been mixed. For example, numerous studies have not found higher speciation or diversification rates in tropical regions (e.g. Wiens *et al.* 2006, Weir and Schluter 2007, Jetz *et al.* 2012, Economo *et al.* 2018, Miller *et al.* 2018, Igea and Tazentap 2020, Tietje *et al.* 2022), whereas others have (e.g. Pyron and Wiens 2013, Rolland *et al.* 2014). Schluter (2016) suggested that this variation might be explained by timescale: studies of older clades showed stronger support for higher diversification rates in tropical regions. Concordantly, simulations (Pontarp and Wiens 2017) found that richness patterns are explained by colonization times in younger clades, and by diversification rates in older clades. An interesting implication of these results is that analyses of recent, species-level speciation and diversification rates may be uninformative for understanding large-scale richness patterns, regardless of their actual causes (Schluter and Pennell 2017).

If diversification rates do not generally explain geographic pattern then what does? A meta-analysis of 15 studies combined

with a systematic review of 15 additional studies (Li and Wiens 2019) found strong support for the idea that geographic richness patterns are typically explained by colonization time (time-for-speciation effect; Stephens and Wiens 2003), and not variation in diversification rates or dispersal rates. In the meta-analysis, colonization time was the most important factor explaining richness in 13 of 15 clades (Fig. 5A), and explained (on average) 72% of the variance in richness among regions across all 15 clades (Fig. 5B). Surprisingly, this analysis showed greater support for the time hypothesis among older clades (contrary to Pontarp and Wiens 2017). The systematic review also showed strong support for the colonization-time hypothesis over the diversification-rate hypothesis (13 studies to one, with one study supporting both).

Similarly, an extensive analysis of 111 phylogenetic studies of vertebrates, insects, and plants addressed the causes of the latitudinal diversity gradient (Jansson *et al.* 2013). They found that most sampled clades originated in the tropics, that there was no significant difference in diversification rates between tropical and temperate lineages, and that there were more transitions from the tropics to the temperate zone than vice versa. Thus, their results suggested that higher tropical richness is generally explained by greater time in the tropics, not faster tropical diversification rates or more frequent dispersal to the tropics.

Saupe (2023) recently claimed that spatial richness patterns must be explained by variation in diversification rates and dispersal rates. They verbally rejected the colonization-time hypothesis, but did not address the extensive support for it from other studies (see above).

Overall, colonization time seems to be a widespread explanation for spatial richness patterns. Thus, the time available for speciation after colonization is often more important for explaining geographic richness patterns than rates of speciation alone. Given this, more studies are needed that (minimally) test both hypotheses, and not speciation or diversification rates alone.

### Trait-based patterns

Trait-based richness patterns involve the number of species having each state of a given character, such as diet or sexual reproduction. As a general type of richness pattern, trait-based patterns have often been somewhat neglected, despite excellent studies on specific patterns (e.g. [Burin et al. 2016](#), [O'Meara et al. 2016](#)).

There are three direct (nonexclusive) explanations for trait-based richness patterns within a group of organisms ([Wiens 2023](#)): (i) the most frequent state was associated with faster diversification rates, leading to more species with this state (diversification-rate hypothesis); (ii) there were more transitions to the most frequent state (trait-origins hypothesis, or transition-rate hypothesis); and (iii) the most frequent state evolved earlier in the tree, allowing more time for speciation to build up species richness for that state (trait-age hypothesis). Each of these hypotheses has obvious parallels to those for spatial richness patterns.

A recent review ([Wiens 2023](#)) found that the trait-age hypothesis was most frequently supported ([Fig. 6](#)). That review examined 25 studies (30 traits) that used HiSSE to estimate diversification rates and ancestral states, and that included information on the richness of each state. These included studies of plants ( $N = 13$ ) and animals ( $N = 11$ ). Among these 30 data points, 15 exclusively supported the trait-age hypothesis, eight supported the diversification-rate hypothesis, whereas four supported both, and three supported neither. There was no tendency for the diversification-rate hypothesis to be supported in older studies.

Only some studies have reported transition rates among states. Among these studies, there was only limited support for the transition-rate hypothesis ([Fig. 6B](#)). Unfortunately, it is difficult to estimate the variance in richness explained by trait age, diversification rates, and transition rates, given that the number of data points for trait-based richness patterns is often limited (i.e. typically just two or three character states).

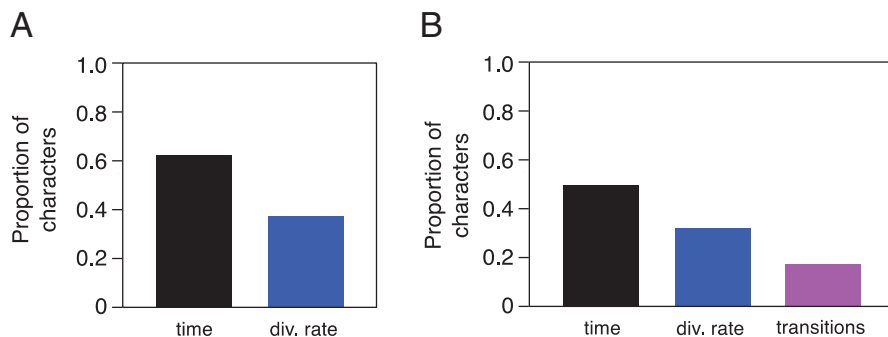
Overall, these results suggest that patterns of trait-based species richness are most often related to the timing when different states arose (with the state that arose earlier likely to be the most species-rich today). However, there were also many studies that supported the diversification-rate hypothesis, and with some support for the transition-rate hypothesis.

### Synthesis

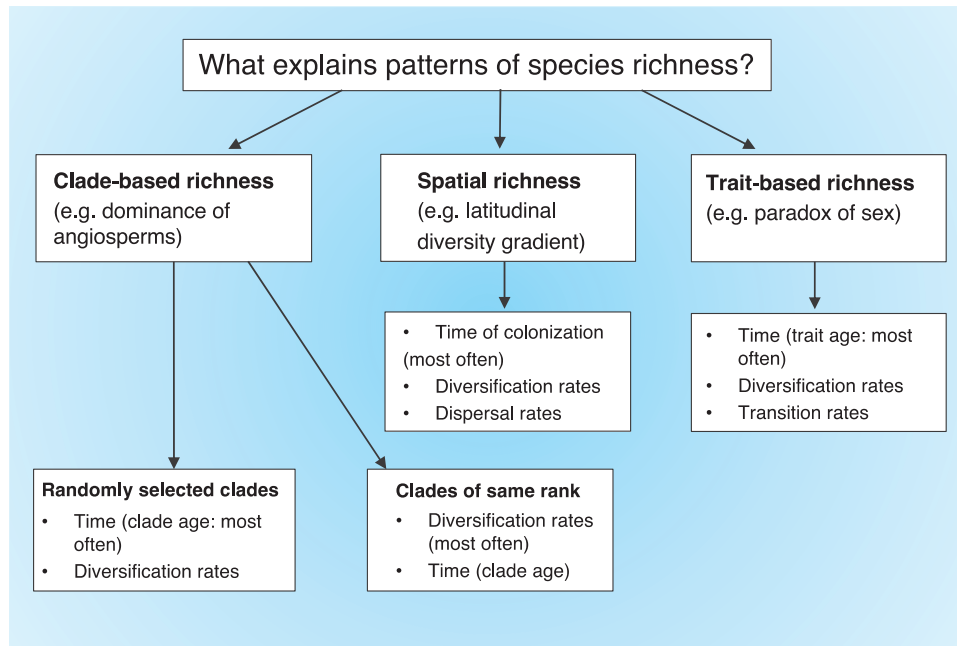
Patterns of species richness must ultimately be related to speciation, the original source of all species richness. However, this review suggests that richness patterns are often unrelated to variation in speciation rates per se ([Fig. 7](#)). Specifically, geographic richness patterns and trait-based patterns are more frequently explained by the time available for speciation: either the time since colonization of a region or habitat or the time since the origin of a given character state ([Fig. 7](#)). Similarly, when clades are selected randomly, then their species richness is generally determined most strongly by their ages ([Fig. 7](#)). For all three of these richness patterns, the transition to a different region, character state, or clade age can happen anywhere in the tree. Under these conditions, time seems to exert a powerful influence on richness patterns. In the simplest case, a very young clade would need to have very rapid diversification rates to generate more species than a much older clade.

On the other hand, when comparing clades of the same taxonomic rank (e.g. phyla to phyla, families to families), then richness patterns are generally explained by variation in diversification rates. Comparing clades of the same rank may tend to restrict the clade ages to be more comparable (e.g. phyla are old, whereas randomly selected clades can be old or very young). These comparisons of clades of the same rank include many of the most dramatic clade-based richness patterns, such as arthropods among animals and angiosperms among plants.

The variation in diversification rates underlying these clade-based richness patterns is often related to traits. Traits related to local-scale ecology and species interactions (alpha niche) seem especially important at deep phylogenetic scales (e.g. pollination



**Figure 6.** The causes of trait-based richness patterns. A, summary of patterns among all 30 characters (25 studies; from table 2 of [Wiens 2023](#)), showing relative support for the trait-age hypothesis (time: oldest state is the most frequent among species) and the diversification-rate hypothesis (div. rate: most frequent state is associated with faster diversification rates). For some characters there was support for both hypotheses. In these cases, we counted the support for each hypothesis as 0.5, as opposed to 1 when a given hypothesis was the only one supported. This allowed the proportions to sum to 1. Three characters in which no hypotheses were supported were not counted when calculating the relative support for each hypothesis. B, summary of patterns among 21 characters for which all three hypotheses were tested (trait age, diversification rate, transition rate) showing the relative support for each hypothesis. In the full set of 30 characters, there were nine characters for which the transition-rate hypothesis was not tested: we excluded these here. For some characters there was support for two hypotheses. In these cases, the support for each hypothesis was counted as 0.5 (as opposed to 1 when a given hypothesis was the only one supported).



**Figure 7.** Summary of the causes of species richness patterns among clades, regions, and traits. Richness patterns can be categorized as clade-based, spatial, or trait-based. All three richness patterns can be directly explained by either variation in diversification rates (e.g. faster rates associated with certain clades, regions, or character states) or by variation in the time available for speciation and diversification (based on the age of each clade, when each region was colonized, or when each character state evolved). Spatial richness patterns can also be explained by dispersal rates among regions and trait-based richness patterns can also be explained by transition rates among states. The statements about which hypothesis explains each type of richness pattern most often are based on the results shown in [Figures 4–6](#).

in angiosperms, herbivory in insects, terrestrial microhabitat among animals and plants) whereas traits related to large-scale ecology and geography (beta niche) seem especially important at shallower scales (e.g. clade range size and rates of climatic-niche evolution among plant and vertebrate families). In some cases, there is evidence to link these traits underlying large-scale patterns to smaller-scale studies of speciation (e.g. for insect pollination and herbivory).

A final point to consider is that most of life may belong to clades with relatively rapid diversification rates (e.g. angiosperms, arthropods, insects). Given this, relatively rapid speciation may be the norm across life, rather than the exception. Thus, ‘typical’ speciation in flowering plants and insects may underlie much of the diversity of life.

#### *Areas for future research*

I suggest several questions as high priorities for future research. (i) We need to understand why some richness patterns are explained by diversification rates and others by time, particularly for geographic and trait-based richness patterns. The idea that older patterns are explained by diversification rates and younger patterns by time seems promising ([Schluter 2016](#), [Pontarp and Wiens 2017](#)), but has not been supported in (at least some) analyses of geographic and trait-based richness ([Li and Wiens 2019](#), [Wiens 2023](#)). (ii) For analyses of clade-based richness, we need to test potential generalizations about the importance of different types of traits (e.g. alpha vs. beta niche traits) more broadly and quantitatively. (iii) It would also be valuable to tease apart the relative effects of speciation and extinction rates on variation in diversification rates among large-scale clades.

For example, do traits that increase diversification do so more often by accelerating speciation or reducing extinction? (iv) For groups in which diversification-related traits have been hypothesized, we need to better link these traits to the evolutionary and ecological mechanisms that drive diversification, such as large range sizes that might buffer clades from extinction or promote allopatric speciation.

## CONCLUSIONS

- (1) In this review, I have addressed two main topics: what might typical speciation be like across life and how did speciation generate the large-scale diversity patterns we see today?
- (2) What typical speciation looks like (i.e. what is most frequent among species) depends on the species richness of different groups.
- (3) Host-associated speciation (co-speciation and host-switching) may be the most frequent speciation processes across life, given that host-associated species of bacteria, protists, fungi, and animals may outnumber free-living species.
- (4) Among free-living animals, three potential generalities about speciation are that it is often allopatric (at least among animals) and frequently involves ecological divergence, and that prezygotic isolation seems to be more widespread and important than postzygotic isolation.
- (5) Despite being widespread across life, we still have an incomplete understanding of allopatric speciation,

especially how sister species become allopatric. Based on first principles, this should involve niche conservatism (i.e. limited adaptation to the ecological conditions separating the geographic ranges of sister species), but this pattern is only rarely tested and only infrequently supported when it is tested.

- (6) Another important area for future research is the processes involved in the origins of cryptic insect species. These species might make up a large proportion of Earth's current macroscopic biodiversity. The review of case studies here suggests that cryptic insect species are often sympatrically distributed, with host-associated divergence also being relatively common.
- (7) All species richness patterns ultimately arise from speciation. These include patterns among clades, among locations, and among traits. The processes underlying these richness patterns can be revealed using time-calibrated phylogenies to estimate rates of speciation and diversification.
- (8) Three major types of methods to estimate these rates include those based on species (e.g. BAMM, ClaDS, MiSSE), clades [e.g. RPANDA, Magallón–Sanderson (MS) estimator], and traits (e.g. HiSSE). These approaches each have their advantages and disadvantages. Among species-level approaches, ClaDS and MiSSE seem especially promising. These new methods allow for extensive variation in speciation rates among and within clades, whereas BAMM does not.
- (9) Some authors have claimed that certain clade-based methods (e.g. MS estimator) cannot resolve the drivers of biodiversity patterns. This claim is based on forcing this method to predict future species richness (an impossible task that it was not designed for nor used for), and no evidence was provided that it performs any worse at this task than other methods. By contrast, simulations show that this method can estimate rates that are strongly correlated with true rates, and empirical analyses show that it estimates rates that are strongly correlated with those from other methods (e.g. ClaDS). This method has also revealed the drivers of biodiversity patterns among clades in many case studies.
- (10) Patterns of species richness among named clades of the same taxonomic rank (e.g. families, phyla) are strongly related to variation in diversification rates. This variation in diversification rates is strongly related to variation in traits. Traits related to the alpha niche (local-scale ecology: like microhabitat and species interactions) seem to be especially important at deep timescales, whereas traits related to the beta niche (large-scale ecology: like range size and climatic niche) are often important at shallower timescales.
- (11) Many other patterns of species richness seem to be related to the time available for speciation more often than to rates of diversification. These other patterns include patterns of richness among clades (when clades are chosen randomly rather than comparing clades of the same taxonomic rank), spatial patterns of richness (such as the latitudinal diversity gradient), and trait-based pat-

terns of richness (the number of species with each character state).

## SUPPLEMENTARY DATA

Supplementary data are available at *Evolutionary Journal of the Linnean Society* online.

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## CONFLICT OF INTEREST

The author declares no competing interest.

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## DATA AVAILABILITY STATEMENT

The data in Supporting Information [Dataset S1](#) will be made available online upon acceptance.

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