

Speciation across the Tree of Life

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ABSTRACT

Much of what we know about speciation comes from detailed studies of well-known model systems. Although there have been several important syntheses on speciation, few (if any) have explicitly compared speciation among major groups across the Tree of Life. Here, we synthesize and compare what is known about key aspects of speciation across taxa, including bacteria, protists, fungi, plants, and major animal groups. We focus on three main questions. Is allopatric speciation predominant across groups? How common is ecological divergence of sister species (a requirement for ecological speciation), and on what niche axes do species diverge in each group? What are the reproductive isolating barriers in each group? Our review suggests the following patterns. (i) Based on our survey and projected species numbers, the most frequent speciation process across the Tree of Life may be co-speciation between endosymbiotic bacteria and their insect hosts. (ii) Allopatric speciation appears to be present in all major groups, and may be the most common mode in both animals and plants, based on non-overlapping ranges of sister species. (iii) Full sympatry of sister species is also widespread, and may be more common in fungi than allopatry. (iv) Full sympatry of sister species is more common in some marine animals than in terrestrial and freshwater ones. (v) Ecological divergence of sister species is widespread in all groups, including ~70% of surveyed species pairs of plants and insects. (vi) Major axes of ecological divergence involve species interactions (e.g. host-switching) and habitat divergence. (vii) Prezygotic isolation appears to be generally more widespread and important than postzygotic isolation. (viii) Rates of diversification (and presumably speciation) are strikingly different across groups, with the fastest rates in plants, and successively slower rates in animals, fungi, and protists, with the slowest rates in prokaryotes. Overall, our study represents an initial step towards understanding general patterns in speciation across all organisms.

Key words: animals, bacteria, co-speciation, ecological speciation, fungi, plants, protists, speciation

CONTENTS

I. Introduction	1206
II. Speciation in prokaryotes	1208
(1) What are bacterial species and speciation?	1208
(2) Bacterial species richness and the Pie of Life	1208
(3) Geographic modes in bacteria	1209
(4) Ecological divergence in bacteria	1210
(5) Isolating barriers in bacteria	1210
(6) Host-mediated speciation in bacteria	1210
III. Speciation in protists	1211
(1) Geographic modes in protists	1211
(2) Ecological divergence in protists	1211
(3) Reproductive isolating barriers in protists	1212
(4) Host-mediated speciation in symbiotic protists	1212

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IV. Speciation in fungi	1212
(1) Geographic modes in fungi	1212
(2) Ecological divergence in fungi	1213
(3) Reproductive isolating barriers in fungi	1214
(4) Host-mediated speciation in symbiotic fungi	1214
V. Speciation in plants	1214
(1) Geographic modes in plants	1214
(2) Ecological divergence in plants	1215
(3) Reproductive isolating barriers in plants	1216
VI. Speciation in animals	1216
(1) Molluscs	1216
(a) <i>Geographic modes in molluscs</i>	1216
(b) <i>Ecological divergence in molluscs</i>	1217
(c) <i>Reproductive isolating barriers in molluscs</i>	1217
(2) Insects	1217
(a) <i>Geographic modes in insects</i>	1218
(b) <i>Ecological divergence in insects</i>	1218
(c) <i>Reproductive isolating barriers in insects</i>	1219
(3) Marine invertebrates	1219
(a) <i>Geographic modes in marine invertebrates</i>	1220
(b) <i>Ecological divergence in marine invertebrates</i>	1220
(c) <i>Reproductive isolating barriers in marine invertebrates</i>	1221
(4) Vertebrate speciation	1221
(a) <i>Geographic modes in vertebrates</i>	1221
(b) <i>Ecological divergence in vertebrates</i>	1222
(c) <i>Reproductive isolating barriers in vertebrates</i>	1222
VII. Major generalizations and patterns	1223
(1) Co-speciation and host-switching	1223
(2) Geographic modes of speciation	1224
(3) Ecological divergence and speciation	1225
(4) Reproductive isolating barriers	1226
(5) Rates of diversification and speciation	1227
VIII. Conclusions	1227
IX. Acknowledgements	1228
X. References	1228
XI. Supporting information	1242

I. INTRODUCTION

‘How do new species originate?’ is a fundamental question in biology. Speciation is the process that ultimately generates the diversity of life. Given its importance, there have been many excellent syntheses on speciation, including outstanding books (e.g. Coyne & Orr, 2004; Nosil, 2012) and review papers (e.g. Schluter, 2009; Seehausen *et al.*, 2014).

Nevertheless, we argue that there is an important gap in the empirical literature on speciation, relating to how diverse organisms are treated. Synthetic papers on speciation generally fall into two main classes. First, there are synthetic works focused on particular topics in speciation, including ecology (Schluter, 2009; Nosil, 2012), hybridization (Abbott *et al.*, 2013), and genomics (Seehausen *et al.*, 2014). These syntheses often review papers primarily on animals, or animals and plants. Second there are synthetic works on specific groups of organisms, such as plants (Rieseberg & Willis, 2007; Givnish, 2010), fungi (Giraud *et al.*, 2008), birds (Price, 2008), and insects (Mullen & Shaw, 2014). We believe

that an unfilled gap is to compare speciation explicitly across major groups. For example, is speciation in plants different from that in animals? Is speciation in fungi different from that in plants and animals? What about bacteria and protists? More broadly, can we make generalizations about speciation that are truly general, and apply to all organisms?

Here, we make an initial attempt to fill this gap. In the sections that follow, we first focus separately on speciation in each major group of organisms (i.e. bacteria, protists, fungi, plants, and animals). Following these taxonomic sections, we then present our major conclusions derived from our comparisons across these groups. Given the vast literature in animals (and because animals include most described living species), we focus on four sets of animals: (i) molluscs, (ii) insects, (iii) marine invertebrates, and (iv) vertebrates. These represent major groups in the three numerically dominant phyla (Mollusca, Arthropoda, Chordata), and a non-monophyletic assemblage that incorporates most other animal phyla (marine invertebrates). Protists are also not monophyletic, but we lump them for convenience here

(as do other authors; e.g. Pawlowski *et al.*, 2012). Similarly, we do not have a dedicated section on archaeans, but much research on prokaryote speciation focuses on bacteria.

We emphasize three broad questions about speciation for each group. (i) Is allopatric speciation predominant across the Tree of Life? (ii) How prevalent is ecological divergence among sister species (a necessary requirement for ecological speciation), and on what niche axes do sister species diverge in each group? (iii) What are the causes of reproductive isolation among species in each group? For groups in which species often live in association with other organisms (e.g. parasites, endosymbiotic mutualists, and commensals), we also address the relative frequencies of co-speciation and host-switching as speciation mechanisms (see below for definitions). In the final section, we also briefly compare rates of diversification (speciation minus extinction) across groups. To help address these questions, we conducted a systematic search of the literature on each group (see online Supporting Information, Appendix S1, for details of searches for each group).

Why these three main questions? Geographic modes have long been an important topic in speciation research. Major debates focus on whether allopatric speciation is predominant (e.g. Coyne & Orr, 2004), and whether sympatric speciation is possible and if so how frequent (e.g. Berlocher & Feder, 2002; Bolnick & Fitzpatrick, 2007). We note that some researchers have advocated classifying speciation as being with or without gene flow, and ignoring geographic modes (e.g. Fitzpatrick, Fordyce & Gavrilets, 2008, 2009). Nevertheless, estimating the frequency of geographic modes remains an active area of study (e.g. Skeels & Cardillo, 2019), and a simple dichotomy between speciation with *versus* without gene flow also has downsides. For example, this dichotomy ignores the special difficulty of sympatric speciation relative to other geographic modes (e.g. Coyne & Orr, 2004) and that allopatry in particular may require a failure to adapt to the habitat separating incipient species rather than adaptation to divergent habitats (e.g. Wiens, 2004; Hua & Wiens, 2013). Moreover, estimating gene flow between sister species (especially at the time of their splitting) is not necessarily any easier than estimating their geographic overlap, and often requires data that are simply not available for many sister-species pairs. Furthermore, categorizing speciation events as with or without gene flow may also require dividing a continuum into discrete categories (see table 1 in Harrison, 2012), which this approach was intended to avoid. Ecological speciation has become a major topic in speciation research (e.g. Schluter, 2009; Nosil, 2012), so its inclusion needs little justification. Similarly, reproductive isolating barriers are fundamental to speciation (e.g. Coyne & Orr, 2004). However, we acknowledge that the most straightforward comparisons to make across groups involve geographic modes, frequencies of co-speciation and host-switching, and diversification rates, whereas information on reproductive isolating barriers is more heterogeneous across groups.

We infer geographic modes based primarily on geographic overlap of sister species. This approach has been

used widely for decades (e.g. Lynch, 1989; Barraclough & Vogler, 2000; Phillimore *et al.*, 2008; Jezkova & Wiens, 2018). Many studies have also analysed correlations between ages of species pairs and their extent of geographic range overlap (age–range correlations, ARC), to better infer overlap at the time of splitting (e.g. Barraclough & Vogler, 2000). Although this approach has been controversial (e.g. Losos & Glor, 2003), recent simulations suggest that geographic modes are detectable from extant species distributions, even if ranges have shifted over time (Skeels & Cardillo, 2019). Here, we emphasize range overlap of sister species, which is essential for inferring geographic modes (Skeels & Cardillo, 2019). We do not assign sister species with partial range overlap to a geographic mode. Instead, we primarily focus on the number of species pairs that are completely non-overlapping in their distribution (allopatric) and pairs in which one species' range completely overlaps another (sympatric). We acknowledge that one would want additional evidence, beyond range overlap, to infer sympatric speciation strongly (e.g. Coyne & Orr, 2004; Bolnick & Fitzpatrick, 2007). We also note that even inferences of allopatry from simple range overlaps are not guaranteed to be correct, but this caveat is true for most other aspects of evolutionary inference (e.g. phylogeny, divergence times). Moreover, the idea that most presently allopatric species actually arose in sympatry or parapatry seems particularly unlikely.

Along similar lines, we primarily discuss ecological divergence among sister species, a necessary requirement for establishing that these species originated through ecological speciation. Of course, additional information would be necessary to establish that ecological divergence was actually the main driver of speciation in a given case. Importantly, species could diverge ecologically after having originated through other processes, such as mutation-order speciation (Schluter, 2009). Additional evidence that is helpful in linking ecological divergence (in a given variable) to speciation includes: (i) demonstrating that ecological divergence in that variable is involved in reproductive isolation between the species; and (ii) evidence that increased rates of divergence in that variable among species are associated with increased rates of speciation and/or diversification (in that clade). Furthermore, finding support for ecological speciation does not necessarily rule out a role for other processes (e.g. sexual selection and ecological divergence may work together to isolate species; Maan & Seehausen, 2011). Finally, we note that finding that sister species did not diverge ecologically in the traits analysed does not necessarily rule out ecological speciation either, since divergence is only assessed in the ecological traits that were considered. Nevertheless, we assume that researchers in each group of organisms analysed the ecological traits that were most relevant to speciation in the species that they studied, given their expertise.

For species that live in close association with another species (e.g. parasites, endosymbiotic mutualists, and commensals), there are two main mechanisms hypothesized for their speciation: co-speciation and host-switching (e.g. Ricklefs,

Fallon & Bermingham, 2004). In co-speciation, the species splits primarily because its host species does. There may be little ecological divergence for the symbiote in this case. By contrast, under host-switching, the individuals that colonize a new host may be isolated by their occurrence in this new host species.

Finally, we begin our review with a discussion about species concepts in bacteria. We do not present a similar review for every other group of organisms. We contrast prokaryotic and eukaryotic species because most eukaryotic species have sexual reproduction, whereas prokaryotic species do not, and because some authors have questioned whether bacterial species (and speciation) even exist. We think that the study of speciation generally focuses on reproductive isolation between species (e.g. Coyne & Orr, 2004). Importantly, this does not require universal agreement about species concepts, methods of species delimitation, or about what aspects of reproductive isolation are most important to speciation (e.g. geography *versus* ecology *versus* behaviour *versus* genetics). We also include a section on the species richness of bacteria (and other groups), since identifying the most species-rich group of organisms is potentially relevant to which speciation processes are most frequent across living species.

II. SPECIATION IN PROKARYOTES

(1) What are bacterial species and speciation?

A fundamental question in considering speciation across the Tree of Life is whether speciation in prokaryotes (Eubacteria, Archaea) is even comparable to that in eukaryotes. A more basic question is whether bacterial species and speciation actually exist, or whether they are simply a ‘myth’ (e.g. Lawrence & Retchless, 2010).

Prokaryotes do not have gene exchange among individuals associated with reproduction, as in many eukaryotes (Cohan, 2001). Hence, they are generally considered asexual. Thus, gene exchange among conspecific individuals may not seem to be an appropriate basis for species and speciation in prokaryotes.

Nevertheless, there can be gene exchange within and among bacterial species. This can include homologous recombination between closely related individuals and horizontal gene transfer (the latter can occur between distantly related species; Ochman, Lawrence & Groisman, 2000). Fraser, Hanage & Spratt (2007) used simulations to address how recombination could drive bacterial speciation, given that recombination seems to decrease in frequency with greater genetic divergence between individuals. They concluded that high rates of recombination (relative to mutation) can lead to bacterial species that behave like sexual species, with recombination acting as a cohesive force. Bobay & Ochman (2017) argued that because of widespread recombination in bacteria (present in at least half of the surveyed species), bacterial species are generally comparable to those in other organisms.

Shapiro *et al.* (2012) suggested that bacterial speciation may occur when an ecologically homogeneous, recombining population acquires genes that allow use of a novel resource (e.g. host or habitat). Resource-specific genes then sweep through these populations with different ecologies. Finally, the most recent recombination events tend to occur more frequently within rather than between these two sets of populations, leading to bacterial species with similarities to eukaryotic species (i.e. with conspecific individuals sharing similar ecologies and exchanging genes more frequently than heterospecific individuals). Shapiro *et al.* (2012) found some evidence for this model in marine bacteria. Polz, Alm & Hanage (2013) proposed a similar model, with conspecific populations that diverge ecologically and then become distinct genotypic clusters. They also emphasized gene exchange among bacterial lineages sharing the same environment.

Similarly, Cohan (2001) argued that across life, individuals fall into more-or-less discrete clusters (species) on the basis of phenotypic, ecological, and genotypic characteristics. In bacteria, distinct sequence clusters correspond to distinct ecotypes. These ecotypes are made cohesive by periodic selection. Cohan (2016) argued that there is evidence for homogenizing selection in bacterial populations over time (Bendall *et al.*, 2016). Other authors (e.g. Gevers *et al.*, 2005) have also noted that ecological divergence may be key to recognizing distinct bacterial species.

Doolittle & Papke (2006) reviewed diverse opinions on whether bacterial species are real or not. They concluded that sometimes bacterial species are clear and unambiguous and sometimes not. This continuum in species distinctness has also been noted in eukaryotes (e.g. de Queiroz, 2007). Thus, the presence of this continuum is not unique (nor disqualifying) to putative bacterial species.

Overall, we recognize that there is controversy about the existence of bacterial species and speciation. However, we treat them as potentially comparable to eukaryotic species here, as have other authors broadly interested in speciation (e.g. Coyne & Orr, 2004).

(2) Bacterial species richness and the Pie of Life

The frequency of speciation processes across living organisms may depend heavily on which groups of organisms are the most species rich. Following Larsen *et al.* (2017), we speculate that most living species are likely to be bacteria associated with animal hosts (especially insects, which make up the majority of described animal species). Those authors estimated the minimum number of unique bacterial species per insect host species by examining the distribution of bacterial species among closely related insect species. They found usable data in three genera from two of the largest insect orders (Diptera: fruit flies: *Drosophila*; Hymenoptera: ants: *Cephalotes* and wasps: *Nasonia*). They focused only on closely related insect species given that these species should share the most bacterial species, and thus provide the most conservative estimates of species-specific bacterial richness. They

also showed that high bacterial richness and host specificity in each insect host species were widespread across insects (e.g. Yun *et al.*, 2014). However, the conclusions of Larsen *et al.* (2017) were recently challenged by Louca *et al.* (2019). This will be addressed in detail elsewhere (Wiens, 2021). Below, we briefly show that the calculations of Louca *et al.* (2019) were demonstrably incorrect and that the overall projections of Larsen *et al.* (2017) may be more likely to be correct.

Louca *et al.* (2019) correctly pointed out that Larsen *et al.* (2017) merely estimated the number of unique bacterial species per insect host species, rather than counting them directly. Louca *et al.* (2019) then presented their own indirect estimates of bacterial diversity, using a different approach. They did this only for ants (*Cephalotes*). Moreover, Louca *et al.* (2019) incorrectly assumed that the estimates of Larsen *et al.* (2017) were drawn randomly from among all 130 *Cephalotes* species (they were only for seven closely related species in two clades). Louca *et al.* (2019) estimated that there were only 40.1 bacterial species in total among all 130 species of *Cephalotes*.

This estimate is demonstrably incorrect. The estimates of Larsen *et al.* (2017) for *Cephalotes* were based on data from Sanders *et al.* (2014). Using the standard 97% cut-off for distinct bacterial species, the data of Sanders *et al.* (2014) show 616 bacterial species among the 25 sampled *Cephalotes*. Among these 616 species, relatively few (only 77) were shared with the three other closely related ant genera they sampled. Among the 539 bacterial species found only in *Cephalotes*, most (369) were found in a single host species. In summary, there are at least 616 bacterial species among only 25 sampled *Cephalotes* species, not 40 among all 130 species.

Louca *et al.* (2019) then applied this underestimate for *Cephalotes* to all animal species (excluding without explanation the other insect genera analysed by Larsen *et al.* 2017). They first calculated 65 million bacterial species, based on one estimate of animal richness from Larsen *et al.* (2017; 163 million) and an average of 100 species per animal genus. Louca *et al.* (2019) then estimated only 3 million bacterial species using an older, smaller projection of animal richness (Mora *et al.*, 2011).

They then reduced this estimate to only 40100 host-associated bacterial species across all animals, by assuming that bacterial species can be shared between any pair of animal host genera, regardless of the host's phylogeny, habitat, diet, or geographic range. Thus, they implicitly assumed that (for example) a terrestrial insect herbivore endemic to Europe could share gut endosymbionts with a deep sea fish in the Pacific Ocean. By contrast, Sanders *et al.* (2014) used data from *Cephalotes* ants (and three related genera) to show that microbial biotas within insect species tend to cluster based on host phylogeny, with microbiotas of different genera being the most distinct. Indeed, among 1019 bacterial species they sampled from these four ant genera, only 77 species were shared between *Cephalotes* and any of the other genera. Again, Louca *et al.* (2019) based their estimates of host-associated microbial diversity only on *Cephalotes*.

Thus, we disagree with the conclusion of Louca *et al.* (2019) that there are only 40100 bacterial species among >1 million

insect species. In the one group of insects they considered, there were 1019 bacterial species among only four insect genera (30 sampled species), with many bacterial species found in a single insect host species. These results may not be atypical. For example, a survey of 31 species of lycaenid butterflies found a total of 1156 bacterial species among them (Whitaker *et al.*, 2016). Similarly, a study of 13 species of native Hawaiian insects (including beetles, flies, and true bugs) found 1094 bacterial species (Poff *et al.*, 2017). An analysis of gut microbiotas from 62 diverse insect species found 2073 bacterial species (Colman, Toolson & Takacs-Vesbach, 2012). Yun *et al.* (2014) sampled 218 insect species among 21 insect orders, and found 9301 unique bacterial species, with 46% found in a single sampled insect species. These results are inconsistent with the estimate of only 40 bacterial species per 130 insect host species by Louca *et al.* (2019), and their estimate of 40100 host-associated bacterial species in total.

Finally, re-estimates of species-specific bacterial species for all three insect genera analysed by Larsen *et al.* (2017), based on direct counts, yields a mean bacterial richness per insect host species of 7.6 species/host (*Drosophila* = 6.4; *Cephalotes* = 7.1; *Nasonia* = 9.3). This is lower than the estimate of 10.7 made by Larsen *et al.* (2017), but nevertheless similar. Moreover, the number of species-specific bacteria is only a minimum estimate of overall host-associated bacterial richness. Most importantly, plugging this new mean value into the calculations for global biodiversity from Larsen *et al.* (2017) still supports the idea that most species of living organisms are bacteria associated with animal hosts, and that bacteria dominate the Pie of Life (Wiens 2021). Specifically, Larsen *et al.* (2017; their tables 1–4) projected 0.209 to 5.8 billion species on Earth, of which 66–91% are bacteria, whereas the re-estimates project 0.183 to 4.2 billion of which 58–88% are bacteria (Wiens, 2021). Thus, in order to understand the most frequent processes underlying speciation across life, it is crucial to understand how bacteria speciate, especially those associated with animal hosts (see Section II.6 below).

(3) Geographic modes in bacteria

There has been debate over whether allopatric speciation is widespread in bacteria (Whitaker, 2006). A traditional view is that all bacterial species occur everywhere, and that differentiation is based primarily on environmental differences (e.g. Baas Becking, 1934). Allopatric differentiation has been found in some taxa, but may depend on the marker used. The commonly used 16S ribosomal gene may evolve too slowly to detect recent genetic divergence (Whitaker, 2006). Whitaker (2006) reviewed studies that incorporated additional markers (with or without 16S), and found a mixture of geographic patterns among 11 bacterial genera. Differentiation based primarily on geography alone (i.e. allopatry) was found in six genera, three of which occurred in geothermal hot springs, two in soil, and one in haloalkaline lakes. By contrast, two genera showed genetic divergence among

environments at 'local' scales (40–50 km), with one in soil and another in a freshwater stream. Two species were apparently globally distributed without genetic divergence (both marine), as was one genus occurring in hot springs. Subsequent studies have also supported allopatric speciation in prokaryotes. For example, Reno *et al.* (2009) found strong evidence for allopatric divergence among populations of *Sulfolobus islandicus*, a thermoacidophilic archaeon. Unfortunately, the available studies did not allow for straightforward counts of range overlap among sister-species pairs, in contrast to most macroscopic groups.

Overall, these studies support the idea that bacterial species can be cosmopolitan, allopatric, or occur in nearby distinct habitats. However, more studies will be needed to show robust patterns in geographic modes, after accounting for potential differences due to different habitats. Nevertheless, allopatric speciation might occur frequently in bacteria, as in other organisms.

(4) Ecological divergence in bacteria

Numerous authors have argued that ecological divergence may be an essential part of bacterial speciation (e.g. Cohan, 2001, 2002; Vos, 2011; Polz *et al.*, 2013; Lassalle, Muller & Nesme, 2015). For example, Vos (2011) found evidence for greater ecological divergence associated with greater genetic divergence in bacteria, including both putative within-species and between-species comparisons. This is one of the few quantitative analyses relating ecological divergence and speciation in bacteria. Unfortunately, we found few studies that addressed ecological divergence of bacterial sister-species pairs.

Case studies in free-living bacteria included divergent clades associated with different soil types in *Bacillus* in Death Valley (Connor *et al.*, 2010). In the marine bacterial species *Vibrio cyclitrophicus*, Shapiro *et al.* (2012) found recently diverged populations associated with differently sized zoo- and phyto-plankton (and other organic particles) in sea water. Lassalle *et al.* (2015) reviewed case studies of possible ecological speciation in bacteria, but in many cases the ecological differences were somewhat unclear, and were inferred from genomic patterns of divergence (i.e. reverse ecology).

Similar to Shapiro *et al.* (2012), Retchless & Lawrence (2012) suggested that bacterial speciation involved ecological transitions (facilitated by horizontal gene transfer) followed by selection on substitutions in the new environments. These substitutions then reduce the possibility of recombination with other bacterial lineages. They showed empirical results that offered some support for this model. Overall, there seems to be broad agreement that ecological divergence is generally important for bacterial speciation (even if not ubiquitous). However, one potential issue is that if bacterial species are defined based on ecological divergence, then detecting speciation without ecological divergence may be difficult (but see discussion of allopatry in Section II.3).

(5) Isolating barriers in bacteria

Here, we briefly review isolating barriers in prokaryotes (see also Barraclough, 2019). Overall, there may be two key aspects of genetic isolation of prokaryotic species: separation into distinct environments (see Section II.4), and the development of barriers to recombination. Ecological divergence is thought to be a major driver of speciation in bacteria. This can drive divergent selection between lineages in different environments (as in eukaryotic systems) and might also restrict the lineages that engage in genetic exchange to those occurring in the same environment (e.g. Polz *et al.*, 2013).

Much literature on bacterial speciation has addressed how barriers to recombination could drive bacterial speciation (e.g. Fraser *et al.*, 2007; Polz *et al.*, 2013; Schmutzer & Barraclough, 2019). Most importantly, recombination seems to decrease in frequency with greater genetic divergence between individuals (e.g. Falush *et al.*, 2006; Hanage *et al.*, 2006). This pattern appears to be caused (at least in part) by the protein Rec-A (recombination protein A), which initiates recombination between individuals with a certain level of sequence similarity, and the protein MutS (mutator S), which inhibits recombination between sequences that are too dissimilar (e.g. Vulic, Lenski & Radman, 1999). Simulations suggest that reduced recombination may be important in those clades with relatively high recombination rates (Schmutzer & Barraclough, 2019). However, this mechanism may not apply to prokaryotic lineages that have little or no homologous recombination, including archaeans and many bacterial species (e.g. Polz *et al.*, 2013; Barraclough, 2019). Ecological divergence may be crucial in these lineages instead.

Other isolating barriers may also be important. For example, bacteria can use pheromones to communicate among individuals, which may impact their reproductive isolation among species. Carolo *et al.* (2009) found genetic divergence between individuals with different forms of a signalling peptide, suggesting reproductive isolation between them. This may be a type of prezygotic isolating barrier.

The relative importance of different barriers in prokaryotes remains unclear, and may depend on the clade. This is hardly unique to prokaryotes. Yet, most prokaryote richness may occur inside of eukaryotes, a possibility that is not addressed in most of the literature on bacterial speciation (e.g. Barraclough, 2019). We address this below.

(6) Host-mediated speciation in bacteria

The frequency of different speciation modes and mechanisms in bacteria may ultimately depend on where most bacteria occur. Much literature on bacterial speciation has implicitly assumed that bacteria are free-living (see Section II.1). However, it is possible that most bacterial species richness is inside eukaryotes. For example, each insect species may contain several host-specific bacterial endosymbionts (see Section II.2).

In Table 1, we review the relative frequency of co-speciation between bacteria and their hosts (see Appendix S1 for methods used to find case studies). This review was based on 12 studies that compared the phylogenies of bacterial symbionts and hosts. Across studies, the number of congruent nodes between host and bacterial trees ranged from 50 to 100% (mean = 78.9%). These results suggest that in endosymbiotic bacteria, most speciation events may be caused by the splitting of their host species. Although additional evidence would be useful to establish co-speciation firmly in each case, these results are consistent with the idea that co-speciation may be widespread. This idea is also supported by studies showing that the microbiotas of insect species (and other organisms) are strongly related to the phylogeny of their hosts (e.g. Colman *et al.*, 2012; Yun *et al.*, 2014), especially among closely related host species (Sanders *et al.*, 2014).

This survey might also be biased in some ways. For example, scientists may be more likely to compare phylogenies in systems predisposed to show congruence (e.g. gut endosymbionts). Other studies have shown more complex patterns (Thao, Gullan & Baumann, 2002; Donovan *et al.*, 2004; Kikuchi, Meng & Fukatsu, 2005). Furthermore, many host species may contain multiple bacterial clades that are not closely related. Thus, one clade may show a pattern of congruence, even though all bacteria in the gut (for example) are not each other's closest relatives (i.e. a single clade). This idea is consistent with our survey, showing a combination of co-speciation and host-switching in most groups, but with co-speciation prevalent among the most closely related species.

III. SPECIATION IN PROTISTS

(1) Geographic modes in protists

We conducted systematic searches of the literature on protist speciation (details in Appendix S1) to find relevant case

studies on geographic modes, ecological divergence, and other topics. Historically, each species of protist was thought to live everywhere on Earth that had a suitable environment, in contrast to most species of plants and animals (i.e. 'everything is everywhere, but the environment selects'; Beijerinck, 1913; Baas Becking, 1934; Fenchel & Finlay, 2004; Bass & Boenigk, 2011). Although this idea implies that allopatry is not relevant for protist speciation, very few studies have addressed their geographic modes. Two relevant studies suggest that allopatric speciation does occur in protists. First, Kamiya *et al.* (1998) found support for allopatric speciation in a sister-species pair of *Caloglossa* (Rhodophyta) with non-overlapping ranges. Second, Pereyra *et al.* (2009) suggested that a sister-species pair in *Fucus* (Phaeophyta) diverged in allopatry, after the opening of the Baltic Sea. However, their current distributions partially overlap (Pereyra *et al.*, 2009). These two studies do suggest that allopatric speciation may occur in protists, but more studies are clearly needed on this topic. We found no large-scale examples of sympatry or parapatry of sister species (but see Section III.2). Overall, too few relevant studies are available to allow estimating the frequencies of different geographic modes in protists.

(2) Ecological divergence in protists

Ecological divergence potentially associated with speciation has been described in many free-living and symbiotic protists, especially in marine lineages (e.g. Choanoflagellata, Chlorophyta, Chrysophyceae, Ciliophora, Foraminifera, Phaeophyta). Below, we review some of the niche axes on which sister species have been found to diverge in different protist clades. Lazarus (1983) found partitioning between foraminiferan species in the water column, potentially related to salinity differences. Ecological divergence of 13 foraminiferan sister morpho-species was associated with concentration gradients of nutrients driven by coastal upwellings (Secars, Darling & Wade, 2012). Wylezich *et al.* (2012) suggested that

Table 1. Summary of congruent and incongruent nodes in comparisons of phylogenetic trees between bacterial symbionts and their hosts. The frequency of congruent nodes is the estimated percentage of co-speciation events relative to host-switching events. Note that Thao *et al.* (2000) and Spaulding & von Dohlen (2001) both involve psyllid plant lice, but their taxon sampling is only partially overlapping. Thao *et al.* (2000) only considered nodes that were strongly supported

Host	Congruent	Incongruent	Ambiguous	Reference
Acanthosomatid stinkbugs	8/11 (73%)	3/11	0/11	Kikuchi <i>et al.</i> (2009)
Nycteribiid flies	6/7 (86%)	1/7	0/7	Hosokawa <i>et al.</i> (2012)
Psyllid plant lice (Hemiptera)	5/10 (50%)	5/10	0/10	Spaulding & von Dohlen (2001)
Sepiolid squid	4/6 (67%)	1/6	1/6	Nishiguchi <i>et al.</i> (1998)
Glossinidae (tsetse flies)	5/5 (100%)	0/5	0/6	Chen <i>et al.</i> (1999)
Aphids (genus <i>Uroleucon</i>)	5/8 (62%)	2/8	1/8	Clark <i>et al.</i> (2000)
Dryophthorid beetles	7/10 (70%)	3/10	0/10	Lefevre <i>et al.</i> (2004)
Carpenter ants	6/12 (50%)	3/12	3/12	Sauer <i>et al.</i> (2000)
Psyllid plant lice (Hemiptera)	9/9 (100%)	0/9	0/9	Thao <i>et al.</i> (2000)
Plataspid stinkbugs	7/7 (100%)	0/7	0/7	Hosokawa <i>et al.</i> (2006)
Aphids (multiple genera)	9/9 (100%)	0/9	0/9	Moran <i>et al.</i> (1993)
Cockroaches	8/9 (89%)	1/9	0/9	Lo <i>et al.</i> (2003)

establishment and subsequent divergence of a single species pair of marine choanoflagellates was associated with changes in mitochondrial cristae, which influence tolerances to hypoxic conditions. Tucker (2013) proposed that horizontal gene transfer allowed some choanoflagellate species to exploit novel environments (i.e. nutrient-poor conditions). Divergence between a sister-species pair within Chrysophyceae (*Ochromonas*) and one within Ciliophora (*Oxytricha*) were associated with tolerances to different pH regimes (Weisse *et al.*, 2011). In ciliates, closely related species may diverge in their salinity distributions (Stock *et al.*, 2013).

Ecological divergence in symbiotic protists is only rarely addressed. Thins *et al.* (2009) found that divergence of one species pair in the oomycete genus *Albugo* was associated with physiological tolerances to different hosts. Other studies have addressed the roles of host-switching and co-speciation (see Section III.4).

In summary, among the 17 sister-species pairs of protists reviewed here, 100% showed some sort of ecological divergence. Furthermore, in almost all of these pairs (94%; 16/17) the ecological divergence involved separation along abiotic habitat gradients (e.g. nutrients, pH, oxygen concentration). This might also suggest that at least some pairs may have evolved in large-scale sympatry or small-scale parapatry, but further studies are needed to test this (Weisse, 2007).

(3) Reproductive isolating barriers in protists

Most studies on intrinsic reproductive barriers have focused on free-living protists. Below we summarize the barriers among sister species found in different clades. Within the *Cryptocodium cohnii* species complex (Dinzoa), gametic incompatibility between morphologically similar strains correlated with physiology (e.g. radiation response) and structural differences in DNA (e.g. doubling time, chromosome number; 1 sister pair; Beam & Himes, 1977). Coleman (2001) found genetic clusters in *Pandorina* algae (Charophyta) that were sexually isolated through gametic incompatibility (15 sister pairs). Prezygotic isolation through gametic incompatibility has been reported in many other diatoms (1 sister pair: Chromalveolata: *Pseudonitzschia*; Amato *et al.*, 2007), and *Paramecium* (14 sister pairs: Ciliophora; Coleman, 2005). Polyploidization appears to be an important isolating barrier in some ciliates (1 species pair; Aury *et al.*, 2006), and algae (Ramjee & Sarma, 1971), including *Micrasterias* (2 sister pairs: Charophyta; Poulíèková *et al.*, 2014), and *Antithamnion* (1 species pair: Rhodophyta; Maggs *et al.*, 2011). Clonal reproduction is also an isolating barrier in brown algae (Phaeophyta; 1 species pair; Pereyra *et al.*, 2009). Hybrid sterility, a form of postzygotic isolation, has been documented in red algae (Rhodophyta; Niwa, Kobiyama & Sakamoto, 2010).

Gametic incompatibility also appears to be widespread in symbiotic protozoa. In *Plasmodium berghei* (Apicomplexa), the absence of certain proteins in female gametes increases hybridization with *P. yoelii* males (1 species pair; Ramiro *et al.*, 2015). In *Trypanosoma* (Excavata), reproductive isolation is primarily controlled at the level of gamete fusion (Peacock

et al., 2014). Pre-mating isolation, examined using *in vitro* experimentation, is the most frequently reported barrier in oomycete plant pathogens [review in Restrepo *et al.* (2014), table 1]. Finally, closely related symbiotic dinoflagellates appear to be isolated by ploidy changes (Loeblich, Schmidt & Sherley, 1981; Blank & Trench, 1985) or host specificity (Lajeunesse & Thornhill, 2011).

Overall, the exact frequency of each isolating barrier among protist species remains unclear. However, prezygotic isolation through gametic incompatibility and polyploidy seem to be especially widespread (86 and 11%, respectively, of 37 species pairs examined here).

(4) Host-mediated speciation in symbiotic protists

The relative roles of co-speciation and host-shifting in symbiotic protists may depend on the group of protists and their ecology. Co-speciation appears to be predominant among sampled members of Excavata, whereas host-switching is more common among Apicomplexa. Specifically, Noda *et al.* (2007) found support for 28 co-speciation events and a single host shift among excavatans living in termites. In Apicomplexa, some studies have found frequent co-speciation in *Plasmodium* species associated with primates [co-speciation = 1, host-shifts = 0 (Hughes & Verra, 2010); co-speciation events = 3–5, host-shifts = 2–4 (Garamszegi, 2009)]. Conversely, among avian- and bat-associated *Plasmodium*, host-switching is far more common [co-speciation = 0, host-shifts = 1 (Waters, Higgins & McCutchan, 1991); co-speciation = 8, host-shifts = 50 (Ricklefs *et al.*, 2004); co-speciation = 0, host-shifts = 13 (Duval *et al.*, 2007)]. Intriguingly, host-shifting seems to occur more often in symbiotic protists associated with highly mobile birds and bats, relative to less-vagile hosts (e.g. termites, primates). In summary, host shifting seems to be the dominant process driving speciation among symbiotic protists, accounting for 62% of 109 speciation events sampled here (Fig. 1). Nevertheless, more studies are needed to estimate how the frequencies of these processes vary based on symbiote clades and/or host ecology.

IV. SPECIATION IN FUNGI

(1) Geographic modes in fungi

To estimate the relative prevalence of different geographic modes in fungi, we conducted a systematic literature search (see Appendix S1 for methods). Among 55 sister-species pairs found (Appendix S2, Table S1), 13 were allopatric (23.6%), 14 fully sympatric (25.5%), 19 partially sympatric (34.5%), and 9 parapatric (16.4%). Sampling was dominated by pathogens (27 pairs, 49%) and fungi with conspicuous fruiting bodies (11 pairs, 20%). Only the two most species-rich phyla (Ascomycota, Basidiomycota) were represented. The prevalence of sympatric pairs contrasts with Kohn (2005), who suggested that allopatric speciation is more common, based on mushroom-forming Basidiomycota. Among sampled

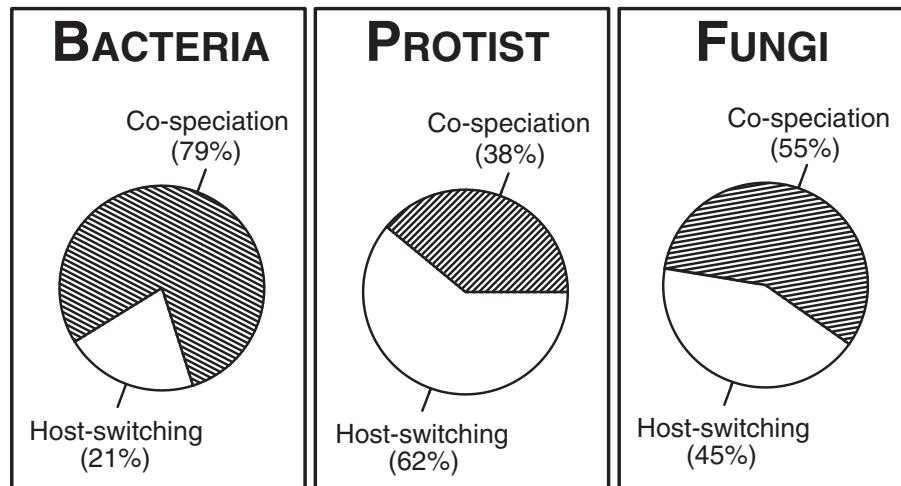


Fig. 1. Relative frequencies of co-speciation and host-switching in symbiotic bacteria, protists, and fungi. Values for bacteria are based on Table 1 (mean across studies), with a total sample size of 103 speciation events. Values for protists are based on the overall frequency of modes across all reported events (co-speciation and host-switching; $N = 109$). For those studies reporting a range of values, the midpoint of the range was used. Within protists, Excavata and Apicomplexa show very different values, with Excavata dominated by co-speciation (96%, $N = 29$ events total) and Apicomplexa dominated by host-switching (84%, $N = 80$). Values for fungi are based on the midpoint of the ranges of estimates from the six studies summarized here, with the overall values based on the mean across studies. The overall number of speciation events (from the sum of the midpoints for each mode and study) is $N = 157$.

Basidiomycota, we found allopatric pairs were indeed most common: of 13 species-pairs, five were allopatric (38.5%), two fully sympatric (15.4%), four partially sympatric (30.8%), and two parapatric (15.4%). Giraud *et al.* (2008) argued that sympatric speciation is rare in fungi. Nevertheless, our survey found more fully sympatric pairs than allopatric pairs. Interestingly, most (30/33, 91%) sympatric and partially sympatric sibling species were not host-specific symbionts, in which host shifts or co-speciation provide an easy explanation for reproductive isolation and divergent adaptation.

(2) Ecological divergence in fungi

Studies of potential ecological speciation are rare in fungi (Douhan *et al.*, 2008). Using the search terms “fungi” and “ecological speciation” (Google Scholar, June 2019), we identified five case studies in which the authors proposed that adaptation to divergent environments led to reproductive isolation and speciation. In two cases, plant pathogenic fungi were reproductively isolated by adaptation to different host species. In the other three cases, ‘phylopecies’ were isolated by habitat characteristics, notably temperature. Phylopecies refers to morphologically cryptic species that are revealed by molecular phylogenetic analyses within traditional, morphology-based fungal species (Taylor *et al.* 2000). We restricted this analysis to species pairs that show molecular divergence and limited gene flow, even if they are not formally described.

Among symbiotic fungi, ecological speciation can occur when populations adapt and specialize to different hosts. In *Ascochyta*, species are highly specialized to a given host species and unable to infect others, but they are otherwise fully

intercompatible and produce viable offspring (Peever, 2007; Restrepo *et al.*, 2014). However, the progeny are unable to infect the parental host species, leading to isolation from parental populations (Peever, 2007). Stukenbrock *et al.* (2010) found that *Zymoseptoria tritici* was more pathogenic on wheat than its relatives and there was no evidence of gene flow between isolates since the domestication of wheat. Some authors have proposed that many plant pathogens emerged as a result of ecological speciation *via* adaptation to divergent host plants (Giraud, Gladieux & Gavrillets, 2010). However, studies often identify cryptic phylopecies within sympatric plant pathogen species complexes that have no clear separation by habitat or host (e.g. Queloz *et al.*, 2011). This latter pattern suggests that other barriers to gene flow besides host specialization could be widespread in these fungal symbiotic systems.

Mycorrhizal fungi form close mutualistic symbioses with their plant hosts, but most mycorrhizal fungi are not specialized to a single host species (Bruns, Bidartondo & Taylor, 2002). We found no examples of host-driven speciation in this group. One study suggested that specialization to fungal arbuscular mycorrhizae led to later speciation in the plant hosts: this pattern challenges the widespread assumption that hosts drive the speciation of symbionts rather than the reverse (Merckx & Bidartondo, 2008).

Three studies found evidence for possible speciation through divergent adaptation to different abiotic habitats. Douhan *et al.* (2008) found that in the grass pathogen *Claviceps purpurea*, phylopecies correspond to habitat types of host grasses (dry terrestrial, intermediate, riparian) and not to geography or host species. Bidochka, Small & Spironello (2005) identified sympatric, cryptic phylospecies of the soil-

inhabiting insect pathogen *Metarhizium anisopliae*, and found that isolates segregated into phylopecies according to thermal tolerance, not hosts. Similar patterns were observed in *Beauveria bassiana*, another soil-inhabiting insect pathogen (Bidochka, Menzies & Kamp, 2002), in which isolates from Arctic, forest, and agricultural soil were reproductively isolated, and isolates from agricultural soil required higher temperatures. Dettman *et al.* (2007) and Dettman, Anderson & Kohn (2008) confirmed that reproductive barriers can arise between populations that evolved under divergent experimental conditions *via* antagonistic epistasis.

In summary, in parasitic and pathogenic fungi with narrow host ranges, adaptations to the host were hypothesized to lead to ecological speciation. Furthermore, adaptations to non-host habitats might also lead to ecological speciation in these systems.

(3) Reproductive isolating barriers in fungi

Various isolating barriers have been observed in fungi. Sexual reproduction in fungi is diverse, complex, and poorly understood (Billiard *et al.*, 2012). Further, many fungal species are capable of both sexual and clonal reproduction, and occasionally fungi recombine asexually (Kohn, 2005; Taylor *et al.*, 2015; Stukenbrock, 2016). The relative strength and frequency of pre- and postzygotic reproductive barriers appears to vary by phylum and by life-history traits.

Le Gac & Giraud (2008) analysed data from crossing experiments in 33 fungal species complexes, and found that species pairs in 16 complexes in the Agaricomycetes (Basidiomycota) exhibited strong prezygotic, pre-mating reproductive barriers in sympatry and inconsistent pre-mating barriers in allopatry. By contrast, they found that examined pairs in Ascomycota (primarily plant-pathogenic, 16 complexes) showed only weak and inconsistent postzygotic reproductive barriers in sympatry and allopatry, with limited-to-no pre-mating barriers. Other authors found post-mating barriers in *Neurospora* (Ascomycota) to be stronger between sympatric than between allopatric isolates (Turner, Jacobson & Taylor, 2010).

Work on genomic isolating barriers is largely confined to the model ascomycetes, *Saccharomyces* and *Neurospora*. In these genera, the strength of reproductive isolation is positively correlated with sequence divergence between isolates (Liti, Barton & Louis, 2006; Dettman *et al.*, 2008). This pattern is consistent with the action of the mismatch repair system (which inhibits recombination of divergent individuals), or genetic incompatibilities under the Dobzhansky–Muller model. In both systems, postzygotic isolation, measured as the proportion of viable progeny, was the primary form of reproductive isolation.

Speciation through hybridization has occurred in diverse fungi, and may be more common between allopatric species pairs than sympatric pairs (Steenkamp *et al.*, 2018). Grass endophytes in *Epiclloë* (Ascomycota) hybridize, likely through asexual means *via* the parasexual cycle, and the resulting hybrid lineages are heteroploid and asexual (Moon *et al.*, 2004). The grass pathogen *Zymoseptoria pseudotrifici* arose from a homoploid hybridization event (Stukenbrock, 2016). Under laboratory conditions, all species of *Saccharomyces* are

capable of hybridization, and wild hybrid isolates and hybrid species are common (Hou, Fournier & Schacherer, 2016).

(4) Host-mediated speciation in symbiotic fungi

In order to estimate the prevalence of host-switch speciation and co-speciation, we identified studies that used quantitative co-phylogenetic methods. Jackson (2004) performed co-phylogenetic analyses of 15 fungal species complexes (Basidiomycota and Ascomycota) and their hosts, and inferred that the proportion of co-speciation events ranged from 0.50 to 0.89 across these taxa. All examined parasite–host phylogenies had both co-speciation and host-switch events (Jackson, 2004; Morris & Moury, 2019). We identified six more-recent co-phylogenetic studies of fungal symbionts of plants and other taxa, which each estimated a range of different possible numbers of co-speciation *versus* host-switching speciation events. These included studies of *Microbotryum* parasites of plants (co-speciation = 0–12, host-switching = 0–22; Refrégier *et al.*, 2008), *Anthracoidea* parasites of sedge *Carex* (co-speciation = 7–10, host-switching and lineage duplication within host = 19–22; Escudero, 2015), *Fusarium* mutualists of beetles (co-speciation = 3–4, host-switching = 4–5; O'Donnell *et al.*, 2015), *Cosmospora* parasites of other fungi (co-speciation = 6–7, host-switching = 5–6; Herrera, Hirooka & Chaverri, 2016), *Cyttaria* parasites of *Nothofagus* (co-speciation = 7–8, host-switching = 1–2; Peterson, Pfister & Bell, 2010), and Sclerotiniaceae symbionts of plants (co-speciation = 2–42, host-switching = 31–89; Navaud *et al.*, 2018). One way to summarize these results is to take the midpoint of the range of each study, and summarize these as proportions. This suggests that the frequency of co-speciation ranges from 0.27 to 0.83 among studies (mean = 0.45) and the frequency of host-switching from 0.17 to 0.71 (mean = 0.55). Thus, these more recent studies also suggest that both mechanisms are widespread in fungi.

Non-quantitative comparisons of phylogenies between microsporidian fungi (obligate unicellular parasites) and their insect hosts also suggest that both co-speciation and host-switching are common in this group (Andreadis *et al.*, 2012; Shafer *et al.*, 2009). However, it is difficult to quantify the frequency of the different modes directly from these studies.

V. SPECIATION IN PLANTS

(1) Geographic modes in plants

Botanists have long suggested that sympatric speciation may be more common in plants than in animals (Stebbins, 1950; Grant, 1981). We estimated the frequency of geographic modes based on patterns of range overlap among sister-species pairs (details in Appendix S1). We found 622 sister-species pairs (Table 2), based on previous studies of geographic modes in plants. Among these species pairs, 30.3% were allopatric, 18.1% fully sympatric, and 51.5% partially sympatric. These results suggest that allopatric speciation may be the most frequent mode in plants, but that

Table 2. Summary of estimated geographic modes of speciation for plants. Modes were inferred from geographic range overlap of sister species pairs. In general, range overlap was calculated as the area occupied by both species divided by the area of the smaller-ranged species, ranging from 0 (allopatric) to 1 (sympatric). Intermediate values were considered partially sympatric. Parapatry was not treated as a separate category in most studies (except Price & Wagner, 2004). Instead, this mode is often considered a special case of partial sympatry (van der Niet & Johnson, 2009). Pairs reported as parapatric were counted as partially sympatric here. Frequencies were obtained directly from the references listed or estimated using data reported therein (the latter are marked with an *)

Taxonomic group	Geographic region	Frequency of geographic modes	Reference
Angiosperms (12 families), 71 sister pairs	California Floristic Province	18.3% allopatric, 1.4% sympatric, 80.3% partially sympatric	Anacker & Strauss (2014)
Angiosperms (8 families), 188 sister pairs	Cape Floristic Region	32.9% allopatric, 10.1% sympatric, 56.9% partially sympatric	van der Niet & Johnson (2009)
Sinningieae tribe (Gesneriaceae), 56 sister pairs	Atlantic forest of Brazil	40.8% allopatric, 6.1% sympatric, 53.1% partially sympatric*	Perret <i>et al.</i> (2007)
<i>Piper</i> subgenus <i>Ottonia</i> (Piperaceae), 9 sister pairs	Atlantic forest of Brazil, Amazon and west Andes	22.2% allopatric, 0% sympatric, 77.8% partially sympatric*	Molina-Henao <i>et al.</i> (2016)
Primulaceae, 11 sister pairs	Mountains of the European alpine system	45.4% allopatric, 0% sympatric, 54.5% partially sympatric	Boucher <i>et al.</i> (2016)
<i>Costus</i> (Costaceae), 54 sister pairs	Neotropics	18.5% allopatric, 38.9% sympatric, 42.6% partially sympatric*	André <i>et al.</i> (2016)
<i>Mimulus</i> (Phrymaceae), 24 sister pairs	North America	20.8% allopatric, 37.5% sympatric, 41.7% partially sympatric	Grossenbacher <i>et al.</i> (2014)
Angiosperms, 52 sister pairs	Hawaiian Islands	28.8% allopatric, 42.3% sympatric, 28.8% parapatric (adjacent but non-overlapping)	Price & Wagner (2004)
<i>Banksia</i> , <i>Hakea</i> , <i>Protea</i> (Proteaceae), 122 sister pairs	Australia, South Africa	35.7% allopatric, 23.6% sympatric, 40.8% partially sympatric	Skeels & Cardillo (2019)
<i>Sidalcea</i> (Malvaceae), 8 sister pairs	North America	25.0% allopatric, 37.5% sympatric, 37.5% partially sympatric	Skeels & Cardillo (2019)
<i>Bursera</i> (Burseraceae) 27 sister pairs	Americas	18.5% allopatric, 29.6% sympatric, 51.9% partially sympatric	Skeels & Cardillo (2019)

sympatric speciation may have a similar but lower frequency (see also Skeels & Cardillo, 2019).

(2) Ecological divergence in plants

The role of ecology in speciation in angiosperms was reviewed by Waser & Campbell (2004) and Givnish (2010). Angiosperms include ~90% of land plant species. Pollination is thought to play a fundamental role in ecological speciation in angiosperms. Changes in floral traits and pollination syndromes may be particularly important for reproductive isolation (Waser & Campbell, 2004), especially in combination with other factors (Kay & Sargent, 2009). For example, sympatric and morphologically similar species within *Chiloglottis* (orchids) are known to be reproductively isolated, based on comprehensive nuclear and chloroplast DNA analyses, yet they can only be phenotypically distinguished by floral odour compounds essential for pollinator attraction (Peakall & Whitehead, 2014).

Direct mechanistic links between variation in floral morphology, pollinator shifts, and reproductive isolation have been difficult to elucidate. Schemske & Bradshaw (1999) analysed selection by pollinating hummingbirds and bees on an F₂ hybrid swarm derived from bee-pollinated *Mimulus lewisii* and its sister species, hummingbird-pollinated *M. cardinalis*. They showed that pollinators could create strong divergent selection pressures

for ‘bee’ flowers (low in anthocyanin and carotenoid pigments) and ‘hummingbird’ flowers (rich in nectar and high in anthocyanins). Subsequent work showed that the difference between these flower types is caused by changes in the cis-regulatory region of a single gene, demonstrating that considerable isolation *via* pollinator shift might be due to a single genetic change (Yuan *et al.*, 2013). Studies in *M. aurantiacus* showed that phenotypic differences between closely related ecotypes differing in floral traits are maintained by divergent selection on these traits in this species, despite ongoing gene flow (Sobel & Streisfeld, 2015).

There is also macroevolutionary evidence for the importance of pollination to plant diversification. For example, studies have shown that lineages that utilize biotic pollinators have increased diversification rates relative to those that do not, both across land plants (Hernández-Hernández & Wiens, 2020) and in particular angiosperm groups (e.g. figs; Bruun-Lund *et al.*, 2018). However, future studies should also test whether accelerated plant diversification rates are related to elevated rates of switching among pollinator lineages. For example, floral morphology appears to impact speciation rates in angiosperms (e.g. Sargent, 2004; Hernández-Hernández & Wiens, 2020). Specifically, floral asymmetry may increase pollinator specificity and thus pollinator switching.

How common is ecological divergence in sister species of plants and what traits diverge most frequently? This has been examined quantitatively in South Africa’s Cape floristic

region (van der Niet & Johnson, 2009) and North America's California floristic region (Anacker & Strauss, 2014). In the Cape region, ecological shifts were identified in 80% of 188 sister-species pairs. The most important ecological variables included shifts in habitat (different habitats in 32% of 132 pairs) and pollinators (33% of 173). Changes in soil types were less important (17% of 162). In California, 65% of the pairs had 'complete' shifts in one or more ecological traits (i.e. no overlap between species). The traits that diverged most frequently included habitat, soil type, and flower size, whereas flowering times and chromosome counts differed less often. Although ecological divergence is not necessarily the same as ecological speciation, these results are potentially consistent with the idea that ecological speciation is frequent in plants and often involves habitat type.

(3) Reproductive isolating barriers in plants

Reproductive isolation in plants has been studied mostly in angiosperms. Reproductive barriers in plants can be classified as pre- and post-pollination, equivalent to prezygotic and postzygotic (review in Baack *et al.*, 2015). Pre-pollination barriers (review in Lowry *et al.*, 2008) include immigrant inviability (i.e. lower fitness of immigrants in non-native environments), pollinator behaviour, phenological isolation (disparity in flowering time), and mating system isolation (e.g. evolution of cross or self-fertilization, or apomixis or asexual reproduction, within a population). Post-pollination barriers include pollen competition (i.e. heterospecific pollen has reduced probability of reaching the ovule compared to conspecific pollen), hybrid sterility, and hybrid incompatibilities (Lowry *et al.*, 2008).

There are several factors underlying post-hybridization isolation and hybrid incompatibilities (review in Chen, Zhigou & Lin, 2016). When parents are adapted to different environments (Baack *et al.*, 2015; Chen *et al.*, 2016), hybrids may express intermediate trait values and so have reduced fitness in the parental habitats, causing embryonic inviability (hybrid inviability or lethality), weakness of the vegetative phase in contrast to parents (hybrid weakness), or sterility (hybrid sterility). It has been suggested that selfish genetic elements such as repeat sequences, transposable elements, and meiotic drivers are likely to be the main cause of hybrid incompatibility (Presgraves, 2010; Chen *et al.*, 2016). Recent studies show that hybrid lethality is caused by diverse genes in different species that have been assessed (e.g. *Cif* and *cim* in rice, *MEDEA* in *Arabidopsis*), and might be controlled by multiple loci in each species (Chae *et al.*, 2014; Chen *et al.*, 2016). These results are consistent with the Dobzhansky–Muller model, in which gene interactions cause hybrid lethality.

Recent studies suggest that pre-pollination barriers are often very strong, and typically contribute more to total reproductive isolation in plants than postzygotic barriers [reviews in Lowry *et al.* (2008) and Baack *et al.* (2015)]. Adaptive divergence in response to ecological factors (such as pollinators and habitat) is thought to commonly drive the evolution of prezygotic barriers (Rieseberg & Willis, 2007). However, in contrast to animals, the observation that prezygotic barriers evolve faster than postzygotic barriers has not

been confirmed in plants (Widmer, Lever & Cozzolino, 2009). This could be a consequence of a more complex genetic architecture underlying prezygotic barriers in plants (Widmer *et al.*, 2009). Alternatively, in contrast to animals, plants cannot directly choose their mates but instead depend on pollinators for successful gamete transfer, even though these pollinators are often unreliable (Widmer *et al.*, 2009).

The development of intrinsic postzygotic barriers has been studied extensively in plants, particularly the role of polyploidy. Intrinsic barriers frequently result in polymorphism of incompatibility factors within species (Rieseberg & Willis, 2007). Polyploid speciation, in which the entire genome is duplicated, may be particularly frequent in plants. It is estimated that 15% of speciation events in angiosperms and 31% in ferns are accompanied by ploidy increases (Wood *et al.*, 2009). This high frequency may occur because polyploid plants often exhibit ecological differentiation, local dispersal, high fecundity, perennial life history, and self-fertilization or asexual reproduction (Rieseberg & Willis, 2007).

Speciation by hybridization is also thought to be important in plant speciation (Hegarty & Hiscock, 2005). The frequency of spontaneous natural hybridization varies considerably among different plant genera and families (Ellstrand, Whitkus & Rieseberg, 1996), and is most common among outcrossing species with reproductive strategies that can stabilize hybridity, such as vegetative reproduction, permanent odd polyploidy or agamospermy. Ellstrand *et al.* (1996) concluded that hybrids comprise 6–22% of all angiosperm species.

Plant species are typically isolated not by a single factor, but by a large number of different pre- and postzygotic barriers, and their potentially complex interactions (review in Widmer *et al.*, 2009). By analysing the strength of isolation imposed by several reproductive barriers, Lowry *et al.* (2008) found that each individual barrier is rarely sufficient to cause complete reproductive isolation. Although individual reproductive barriers can arise rapidly, the fact that most plant species remain separated by numerous barriers implies that complete intrinsic reproductive isolation typically requires many thousands of generations. The main exceptions to this are hybrid and polyploid speciation (Rieseberg & Willis, 2007).

VI. SPECIATION IN ANIMALS

There is an enormous literature on animal speciation. Therefore, we divided animals into four sections. We focused on three major clades (molluscs, insects, vertebrates) that are large and well studied. We also include a section on marine invertebrates. Several major phyla are not included here (e.g. Annelida, Nematoda, Platyhelminthes), but initial searches found few studies on speciation in these groups.

(1) Molluscs

(a) Geographic modes in molluscs

To infer geographic modes, we searched the literature and analysed range overlap of sister species (methods in Appendix

Table 3. Summary of estimated geographic modes of speciation in molluscs. Numbers correspond to the number of species pairs with a given pattern of geographic range overlap (percentages represent the frequencies across all relevant pairs). Data are given in Appendix S2, Tables S2–S4

Sister-species pairs	Allopatric	Sympatric	Parapatric	Partially overlapping
Total molluscs	241 (78%)	46 (15%)	8 (2%)	15 (5%)
Marine molluscs	172 (76%)	35 (15%)	5 (2%)	15 (7%)
Freshwater molluscs	11 (73%)	3 (20%)	1 (7%)	0
Terrestrial molluscs	29 (85%)	4 (12%)	1 (3%)	0
island snails	26 (96%)	1 (4%)	0	0
continental snails	3 (43%)	3 (43%)	1 (14%)	0

S1). Sister species from the same region but with uncertain range overlap were not considered. A total of 172 of 227 (76%) sister-species pairs of marine molluscs were allopatric (Table 3). Allopatry was also dominant (73%) in freshwater molluscs (11/15 pairs; Table 3). Land snails have been understudied, except on islands. In archipelagos, 96% of species pairs were allopatric, with most allopatric species endemic to a single island, including Hawai'i (Holland & Cowie, 2009), Belau (Rundell, 2008), and Azores (Jordaens *et al.*, 2009). There were also micro-allopatric pairs within islands (Galápagos: Parent & Crespi, 2006), supporting the idea that terrestrial snails have limited dispersal. We found similar frequencies of allopatric and sympatric pairs in continental terrestrial snails (43% each; Table 3), but based on only seven pairs. Overall (Table 3), we found that most sampled sister species in molluscs are allopatric (78%) and not sympatric (15%) or partially overlapping or parapatric (7% in total).

(b) Ecological divergence in molluscs

Ecological divergence was reported in 18 of 29 pairs (62%) of marine molluscs (Appendix S2, Table S2). Most cases corresponded to habitat divergence (13 pairs), such as physical substrate, salinity/nutrients, bathymetry, and temperature (Table S2). Other cases involved interspecific interactions, such as shifts in coral host species (three pairs), symbiont divergence (one pair), and antipredator metabolism (one pair).

Ecological divergence was reported infrequently in freshwater molluscs (4 of 15 pairs; Appendix S2, Table S3). However, it likely played a role in freshwater species flocks, with divergence associated with habitat (e.g. substrate, bathymetry) and diet (Glaubrecht, 2011). Larval host shifts were reported in two species pairs in Unionidae (Graf, 1997). In terrestrial snails, ecological divergence was supported for one island pair only (Table S4). Ecological divergence was insufficiently studied in continental snails.

(c) Reproductive isolating barriers in molluscs

Isolating barriers have been documented in relatively few molluscs. Post-mating, prezygotic gamete recognition and competition were shown in the marine gastropod genera *Haliotis* and *Tegula*, and the bivalve genus *Mytilus* (Bierne, Bonhomme &

David, 2003; Krug, 2011). Isolation based on different timing of gamete release in different species (pre-mating barrier) occurs in Hawaiian limpets (Bird *et al.*, 2011). Other cases invoke ecological or geographic isolation but the specific barriers are unclear (Table S2). Geographic isolation is associated with reduced dispersal capacities (e.g. non-planktonic larval development), often combined with vicariant refugia or transient allopatry due to changing sea levels (Krug, 2011). Postzygotic barriers (inferred from reduced hybrid fitness) were found in some *Littorina* species (Krug, 2011).

Geographic isolation is dominant in freshwater and terrestrial molluscs (Tables S3 and S4), potentially related to limited dispersal capacities at small scales (e.g. upper *versus* lower portions of streams, bathymetry) and geographic barriers at larger scales (e.g. islands or mountains). Divergence in habitat and diet have been proposed as factors underlying sympatric speciation (Glaubrecht, 2011; Cameron, 2013). There is some evidence for postzygotic barriers (maladaptive hybrids) in *Albinaria* snails (Cameron, 2013). Although shifts between left and right-handedness (chirality) in snail shells has been suggested as a possible mechanism for single-gene speciation in gastropods, the classic case study (Ueshima & Asami, 2003) of this phenomenon in Japanese snails (*Euhadra*) has not been supported by recent analyses (Richards *et al.*, 2017).

(2) Insects

Speciation in insects has been intensively studied. Many review papers are available on different aspects of insect speciation (e.g. Berlocher & Feder, 2002; Matsubayashi, Ohshima & Nosil, 2010; Mullen & Shaw, 2014). We collected information on geographic modes, ecological divergence, and isolating barriers for 231 sister-species pairs (methods in Appendix S1, pairs listed in Appendix S2, Tables S5–S7, and summarized in Table S8). We caution that our review is not comprehensive: we cannot claim to have included all species of insects included in past speciation studies. However, we do have a large sample size of species pairs with which to make some inferences. Many ($N = 30$) of our putative sister-species pairs involved within-species comparisons, including host races of herbivorous insects and subspecies (and other geographic types) of *Drosophila*. Because these include many classic systems in speciation research, we decided to include these in most analyses (but we refer to

Table 4. Summary of estimated geographic modes of speciation and ecological divergence among species pairs of insects. Numbers are numbers of sister-species pairs (and percentages). Data for each pair are given in Appendix S2, Table S8

Sister-species pairs	Allopatric	Sympatric	Parapatric	Partially overlapping
Geographic modes				
All studies	137 (59%)	54 (23%)	9 (4%)	31 (13%)
Current geographic range	56 (41%)	41 (30%)	8 (6%)	31 (23%)
ARC	81 (85%)	13 (14%)	1 (1%)	0
Ecological divergence				
Yes	33 (37%)	34 (38%)	2 (2%)	20 (22%)
with host shift	20 (41%)	18 (37%)	0	11 (22%)
without host shift	3 (14%)	13 (62%)	2 (9%)	3 (14%)
host contribution unknown	10	3	0	6
No	13 (59%)	8 (36%)	1 (4%)	0
Not assessed	91	12	6	11

ARC, age–range correlation.

them as ‘species pairs’ also). We also performed some comparisons excluding these pairs, especially for geographic modes and ecological divergence (to make these results more comparable to other groups). These comparisons yielded similar results. Importantly, these latter analyses also showed that these patterns in insects were robust to excluding dozens of case studies.

(a) Geographic modes in insects

Among the 231 sister-species pairs, 137 (59%) may correspond to allopatric speciation, whereas 54 (23%) were sympatrically distributed (Table 4). For those with range-overlap data only (136 pairs), we found 56 allopatric pairs (41%), 41 sympatric (30%), 8 parapatric (6%), and 31 partially overlapping (23%). For the 95 pairs included in ARC analyses (e.g. Barraclough & Vogler, 2000), 81 pairs (85%) were inferred to be allopatric and only 13 (14%) sympatric and one (1%) parapatric. One reason for these different estimates of sympatric speciation (30 *versus* 14%) is that many currently sympatric pairs may have initiated speciation in allopatry and became sympatric secondarily (Yukilevich, 2014). Another reason is that inconclusive ARC analyses were not used (those with no significant trend, presumably because of mixed speciation patterns; Jiggins *et al.*, 2006). This might inflate ARC-based estimates of allopatric speciation. Nevertheless, both estimates suggest that sympatric speciation is relatively uncommon, as often noted (e.g. Bolnick & Fitzpatrick, 2007). We also performed these overall comparisons after excluding all pairs that were not currently recognized as taxonomically distinct species. This yielded similar frequency estimates (63% allopatric, 19% sympatric; $N = 201$) to those including all 231 pairs (59% allopatric, 23% sympatric).

(b) Ecological divergence in insects

We reviewed evidence for ecological divergence in the same 231 sister-species pairs (see Appendix S1). Insufficient evidence was found for 120 pairs (Table 4). Among the

111 other pairs, ecological divergence was supported in 89 pairs (80%). In other cases (22 pairs, 20%), non-ecological speciation was suggested after extensive study (e.g. Imada, Kawakita & Kato, 2011). We found similar results after excluding intraspecific pairs (divergence in 77%, none in 23%, $N = 88$ total). Ecological divergence might occur under any geographic mode, and it is unclear how geographic modes are related to ecological divergence (Matsubayashi *et al.*, 2010; Nosil, 2012). However, ecological divergence may be necessary for sympatric speciation [e.g. apple maggot fly *Rhagoletis pomonella* (Filchak, Roethele & Feder, 2000); *Timema* walking sticks (Soria-Carrasco *et al.*, 2014)]. Here, we found that most sympatric pairs were ecologically divergent (34/42 pairs; 81%), but so were most allopatric pairs (33/46 pairs; 72%). The majority of pairs with no apparent ecological divergence were allopatric (13/22; 59%).

We also analysed geographic modes among cases of ecological divergence *via* host shift. Host shift has been proposed as a factor underlying sympatric speciation, especially in herbivorous insects (Berlocher & Feder, 2002; Drès & Mallet, 2002). We found that the majority of ecologically divergent pairs had a host shift (49/70 pairs, 70%, including 48/65 herbivorous pairs; Table 4). However, this might be because host shifts may be easier to observe than other types of ecological divergence, and ecological divergence without host shifts may be hidden in pairs that were not assessed for ecological divergence (Table 4). Besides host shifts, other causes of ecological divergence included host adaptation in herbivorous or parasitic species (e.g. phenological or spatial adaptation) and Müllerian mimicry (predator avoidance; Rosser *et al.*, 2015).

Interestingly, the proportion of host shifts in ecologically divergent pairs was higher in allopatric pairs (87%, 20/23 pairs) than sympatric pairs (58%, 18/31 pairs) (Table 4). Our results are concordant with those of Linnen & Farrell (2010), who found that most host shifts occurred in allopatry in *Neodiprion* sawflies. These results suggest that speciation *via* host shift may be as or more common in allopatry than in sympatry.

How precisely herbivory, specialization, and host shifts contribute to speciation is still debated (e.g. Janz, 2011;

Table 5. Summary of inferred reproductive isolating mechanisms among sampled species pairs of insects. Numbers (and percentages) are of sister-species pairs in each category. Unless otherwise stated with 'yes/no' (presence/absence), numbers represent the number of pairs for which the isolation mechanism was found. Details are given in Appendix S2, Table S8

Sister-species pairs	Allopatric	Sympatric	Parapatric	Partially overlapping
Pre-mating isolation				
Total assessed	89	42	6	16
Ecological isolation only	1 (14%)	5 (71%)	0	1 (14%)
Sexual isolation only	2 (20%)	7 (70%)	1 (10%)	0
Both	16 (46%)	17 (49%)	1 (3%)	1 (3%)
Ecological (sexual unknown)	yes: 15; no: 11	9	1	14
Sexual (ecological unknown)	44	4	3	0
Not assessed	48	12	3	15
Post-mating isolation				
Total assessed	22	24	5	7
Prezygotic only	1	2	0	0
Postzygotic only	0	0	0	0
Both	2	1	0	0
Neither	1	2	0	0
Prezygotic (postzygotic unknown)	0	0	0	2
Postzygotic (prezygotic unknown)	18	yes: 17; no: 2	yes: 3; no: 2	yes: 4; no: 1
Not assessed	115	30	4	24

Wiens, Lapoint & Whiteman, 2015; Kergoat, Meseguer & Jousselin, 2017). Forbes *et al.* (2017) reviewed 85 speciation events across seven orders of specialist insect taxa that may have shifted hosts. They found evidence for host-associated genetic structure in 65, host shifts involved in new reproductive barriers in 43, a direct role of host shift in speciation in 26, and evidence that host shifts initiated speciation in 8. The latter result may suggest that host shifts might only rarely initiate speciation, but might instead appear later in the speciation process (e.g. after allopatry).

(c) Reproductive isolating barriers in insects

We also reviewed isolating barriers among the 231 sister-species pairs (Tables S4–S7). Pre-mating isolation was documented in 153 pairs, and insufficiently studied for the remaining 78 (Table 5). Most sympatric pairs (78%; 42/54) had documented pre-mating isolation, presumably reflecting efforts to understand sympatric speciation.

In most pairs that were assessed for both ecological and sexual isolation (i.e. through sexual selection), both were found to have occurred (67%; 35/52). For example, in heliconiine butterflies, wing colour patterns undergo both sexual selection *via* assortative mating and ecological selection. Ecological selection occurs because hybrids with non-parental wing patterns have reduced fitness due to increased predation (Jiggins, 2008). Many pairs are also sexually isolated due to assortative mating *via* host or habitat selection (Matsubayashi *et al.*, 2010). Either ecological isolation alone (7/52, 13%) or sexual isolation alone (10/52, 19%) were less frequent. Sexual isolation is especially well studied in *Drosophila*, which diverge in both courtship behaviour and cuticular hydrocarbons. However, ecological divergence was unclear for most *Drosophila* pairs (Table S6). Both ecological selection

and sexual selection are considered major isolating barriers in insect speciation (Arnqvist *et al.*, 2000; Forbes *et al.*, 2017). Mullen & Shaw (2014) reviewed six model systems at early stages of speciation (*Heliconius* butterflies, *Laupala* crickets, *Rhagoletis* apple maggot flies, *Acyrtosiphon* aphids, *Anopheles* mosquitoes, and *Drosophila* fruitflies). They found that all had multiple simultaneous axes of divergence and associated isolating barriers (e.g. disruptive ecological selection and sexual selection).

Post-mating isolation was studied in only 58 of the 231 pairs, including 22 allopatric and 24 sympatric pairs (Table 5). Postzygotic barriers were found in 45 pairs, and post-mating, prezygotic barriers were found in eight pairs. However, both types were seldom investigated in the same pairs. For those pairs with information for both types, three showed only prezygotic isolation, none had postzygotic isolation only, three had both types, and three had neither. When considering all prezygotic barriers (pre- and post-mating), 79% (42/53) pairs showed both pre- and postzygotic isolation, and 21% (11/53) showed prezygotic isolation only. Coyne & Orr (1989, 1997) found that prezygotic (both pre- and post-mating) isolation is stronger than postzygotic isolation in young *Drosophila* sister species, due to strong prezygotic sexual isolation in sympatric pairs. The dominant post-mating, prezygotic isolation barrier was gametic incompatibility, and the dominant postzygotic barrier was hybrid inviability and/or sterility.

(3) Marine invertebrates

Except for a few species-rich phyla, most major clades of animals are marine invertebrates, including Porifera (sponges; ~8500 described species; Appeltans *et al.*, 2012), Cnidaria (corals, jellyfishes; ~11000 species), and Echinodermata (~7000 species). Many of these phyla share a sessile or

Table 6. Summary of estimated geographic modes in marine and secondarily freshwater invertebrates. Details and references are given in Appendix S2, Tables S9 and S10

Phylum	Habitat	Studies	Sister-species pairs	Allopatric pairs	Partially sympatric pairs	Sympatric pairs
Porifera	Marine	17	25	16 (64.0%)	2 (8.0%)	7 (28.0%)
	Freshwater	1	5	4 (80.0%)	0	1 (20.0%)
Cnidaria	Marine	39	88	53 (60.2%)	5 (5.7%)	30 (34.1%)
	Freshwater	5	12	6 (50.0%)	2 (16.7%)	4 (33.3%)
Placozoa	Marine	1	2	1 (50.0%)	0	1 (50.0%)
Echinodermata	Marine	28	128	98 (76.6%)	8 (6.3%)	22 (17.2%)
Chordata (non-vertebrates)	Marine	18	28	17 (60.7%)	5 (17.9%)	6 (21.4%)
Marine total		103	271	185 (68.3%)	20 (7.4%)	66 (24.4%)
Freshwater total		6	17	10 (58.8%)	2 (11.8%)	5 (29.4%)
Overall total		109	288	195 (67.7%)	22 (7.6%)	71 (24.7%)

relatively immobile adult form, broadcast spawning, limited behavioural complexity, and hermaphroditism (Willis *et al.*, 2006; Bush, Hunt & Bambach, 2016). These factors may influence geographic modes, ecological divergence, and reproductive isolating barriers.

(a) Geographic modes in marine invertebrates

Broadcast spawning poses a paradox for speciation (Palumbi, 1994). First, the marine environment has few obvious barriers to dispersal. Second, pelagic larvae may travel thousands of kilometers. These factors may limit opportunities for allopatric speciation through geographic isolation. Nevertheless, there are thousands of marine invertebrate species (Appeltans *et al.*, 2012). One potential resolution to this paradox is that sympatric speciation is more common in the ocean than on land (Bowen *et al.*, 2013).

We assembled information on 288 sister-species pairs from 109 studies, five phyla, and 15 classes of marine invertebrates (Table 6; details in Appendix S1 and Tables S9, S10). Note that these groups contained a small number of secondarily freshwater members (17 of 288 sister-species pairs), which are included in these counts (but see Table 6). The number of studies for each class was generally proportional to that class' total richness (Pearson's correlation among classes: $\rho = 0.90$, $P < 0.001$). We found that allopatry was dominant overall (68.0% of species pairs). Partially sympatric pairs were uncommon (7.6%). Complete range overlap (sympatry) was not rare (24.7%).

Marine cnidarians had a high frequency of entirely sympatric pairs (34.1% overall; anthozoans = 41.2%, cubozoans = 0%, scyphozoans = 0%, hydrozoans = 32.4%, myxozoans = 66.7%). Thus, sympatric speciation might be the norm in some of these groups. In fact, sympatric pairs of corals were likely underestimated here because we required sister species to be reciprocally monophyletic, and many corals instead show reticulate evolution (e.g. Willis *et al.*, 2006).

An important question is whether sympatric pairs arise from sympatric speciation, or from allopatric speciation and range shifts (Bowen *et al.*, 2013). Coral reefs and other coastal habitats may be especially suited to ecological

speciation in sympatry given strong competition and sharp abiotic gradients in temperature, salinity, and sedimentation (Bowen *et al.*, 2013). However, high dispersal may facilitate secondary sympatry (Knowlton, 1993), and might explain the greater frequency of sympatric pairs in marine groups. This issue could be resolved by using phylogenies to determine if pairs with less range overlap diverged more recently (supporting initial allopatry and subsequent range shifts). Palumbi & Lessios (2005) and Quenouille *et al.* (2011) corroborated this pattern in sea urchins. Further research using this approach should shed light on whether geographic modes differ in marine and non-marine clades.

(b) Ecological divergence in marine invertebrates

Benthic species often diverge across depth gradients (i.e. one sister in shallower water and the other in deeper water), including in corals (e.g. Eytan *et al.*, 2009), echinoderms (e.g. Rogacheva *et al.*, 2013), and ascidians (Dias *et al.*, 2009). Sister species can also diverge in habitat type [e.g. seagrass beds *versus* coral reefs (Carlson *et al.*, 2011); mangroves *versus* reefs (Rutzler, Duran & Piantoni, 2007); open ocean *versus* saline lakes (Dawson & Martin, 2001)]. Pelagic, wide-ranging species may undergo ecological divergence in allopatry or parapatry along thermal gradients (e.g. Schroth *et al.*, 2002). Sister species may also have divergent life-history strategies [e.g. brooding *versus* broadcast spawning (Puritz *et al.*, 2012); colonial *versus* solitary (Tarjuelo *et al.*, 2004)]. These life-history transitions may themselves facilitate speciation, or may be associated with divergence in other ecological factors.

Groups with low dispersal ability may be more likely to diverge ecologically, because local adaptation can be inhibited under extensive gene flow between populations (Knowlton, 1993; Eytan *et al.*, 2009; Pogson, 2016). However, some cosmopolitan species have been revealed to be locally adapted cryptic species complexes (Schroth *et al.*, 2002). The relationships between geographic mode, ecological speciation, and dispersal ability in marine systems form an important area for future investigation.

(c) Reproductive isolating barriers in marine invertebrates

Broadcast spawning is the most common reproductive mode among the invertebrate groups considered here (Bush *et al.*, 2016). The two most important isolating barriers in broadcast spawners are thought to be temporal differences in spawning and gametic incompatibility (e.g. Wolstenholme, 2004; Binks *et al.*, 2012). Famously, in the Great Barrier Reef, >30 coral species spawn together within hours, and >130 spawn in the same month (Harrison *et al.*, 1984). Willis *et al.* (2006) performed experiments showing that heterospecific gametes of Great Barrier Reef corals were usually compatible in the laboratory. Still, they suggested that prezygotic isolating factors must be at work for at least some species, since the frequency of hybridization between congeneric pairs varies widely in nature. A difference in spawning times of a few hours is considered sufficient to maintain isolation between some species, because gametes deteriorate rapidly or become diluted (Fukami *et al.*, 2003; Willis *et al.*, 2006). However, temporal barriers may still be somewhat porous, as implied by frequent reticulate evolution in many coral species (Willis *et al.*, 2006).

Gametic incompatibility is well studied in sea urchins (Palumbi & Lessios, 2005; Lessios, 2011). Bindin is a protein that binds sperm to eggs, and is sometimes called a ‘speciation gene’ because of its potential to create reproductive isolation with minimal genomic divergence (Landry *et al.*, 2003). Gametic incompatibility between congeneric species pairs is not correlated with time since their split but instead with bindin divergence (Palumbi & Lessios, 2005). In addition, bindin shows positive selection in species in sympatry with congenics, but neutral evolution in allopatry (Lessios, 2011). This pattern is thought to be due to assortative mating and sexual conflict (Lessios, 2011).

In broadcast-spawning invertebrates, only a minority of sister-species pairs that were tested show complete gametic incompatibility in the laboratory (e.g. Rahman, Uehara & Pearse, 2001; McClary & Sewell, 2002; Willis *et al.*, 2006; Lessios, 2007). In many cases, pairs show partial incompatibility, where sperm of one species cannot fertilize eggs of the other, but the reverse is unimpeded. Hybrids are less common in nature than expected by laboratory crosses, implicating other prezygotic barriers (Wei *et al.*, 2012). Alternatively, divergent selection against intermediate, hybrid phenotypes may serve as a postzygotic barrier between sympatric, ecologically isolated species whose gametes may easily meet (Rahman *et al.*, 2001; McClary & Sewell, 2002; Willis *et al.*, 2006; Carlon *et al.*, 2011). In addition, hybrid speciation is known in cnidarians (in *Alcyonium* soft corals), in which hybrids become reproductively isolated from both parent species (McFadden & Hutchinson, 2004).

(4) Vertebrate speciation

(a) Geographic modes in vertebrates

To estimate the relative frequency of allopatry *versus* sympatry in vertebrates, we focused on studies performing ARC analyses (Appendix S1). These studies identify sister-species pairs and quantify their geographic overlap.

We collected data for 1627 sister-species pairs from 13 studies, including mammals, birds, squamates, turtles, amphibians, and ray-finned fishes. Of these, 855 pairs (52.6%) were completely allopatric, 601 pairs (36.9%) were partially sympatric, and 171 (10.5%) were fully sympatric (Table 7). Notably, our sample size (1627 pairs) is more than five times that of a similar review (Bolnick & Fitzpatrick, 2007), yet our results

Table 7. Summary of estimated geographic modes of speciation among vertebrates. Allopatric pairs had 0% range overlap, partially sympatric pairs had 1–99% overlap, and sympatric pairs had 100% overlap (species with smaller range size fully overlapping the range of the species with larger range size). We excluded pairs labeled as ‘parapatric’ because these were difficult to distinguish from allopatry across all studies. When the same pair was included in more than one previous study, we only included information from the most recent study (no pairs were counted twice). We excluded pairs from Barraclough & Vogler (2000) because we could not distinguish between sister-species pairs and internal nodes based on their data

Group	Sister species pairs	Allopatric pairs	Partially sympatric pairs	Sympatric pairs	References
Mammals	170	98 (57.6%)	65 (38.2%)	7 (4.1%)	Fitzpatrick & Turelli (2006); Skeels & Cardillo (2019)
Birds	685	365 (53.3%)	310 (45.3%)	10 (1.5%)	Lynch (1989); Chesser & Zink (1994); Phillipore <i>et al.</i> (2008); Skeels & Cardillo (2019)
Amphibians	190	106 (55.8%)	60 (31.6%)	24 (12.6%)	Kozak & Wiens (2006); Hua & Wiens (2010); Wollenberg <i>et al.</i> (2011); Skeels & Cardillo (2019)
Squamates	323	179 (55.4%)	79 (24.5%)	65 (20.1%)	Jezkova & Wiens (2018); Skeels & Cardillo (2019)
Turtles	10	9 (90.0%)	1 (10.0%)	0	Stephens & Wiens (2003)
Ray-finned fishes					
rivers	166	83 (50.0%)	61 (36.7%)	22 (13.3%)	E.C. Miller (in preparation)
lakes	22	1 (4.5%)	0	21 (95.5%)	E.C. Miller (in preparation)
marine	61	14 (23.0%)	25 (41.0%)	22 (36.1%)	Quenouille <i>et al.</i> (2011); Hodge <i>et al.</i> (2013); Skeels & Cardillo (2019)
Total	1627	855 (52.6%)	601 (36.9%)	171 (10.5%)	

are broadly congruent. They counted 309 pairs across animals (mostly vertebrates) and found only ~9% had >90% range overlap, compared to ~72% with no overlap. Overall, our results suggest that allopatric speciation may be the dominant mode among vertebrates, whereas sympatric speciation appears to be much less common.

Results within each vertebrate subgroup also suggest that allopatry may be the dominant mode (Table 7). However, lacustrine and marine fishes seem to be an exception. Almost all lacustrine pairs in our sample were sympatric (95.5%; $N = 21$). All of these pairs were from the family Cichlidae (E.C. Miller, in preparation). Some of the best-supported cases of sympatric speciation in general come from lacustrine fishes, especially cichlids (Seehausen & Wagner, 2014). Among marine fishes, 36% of pairs were fully sympatric, compared to 23% that were allopatric. The prevalence of marine sister-species pairs with large, overlapping ranges and few obvious barriers to gene flow implies that sympatric speciation may be common (Puebla, 2009; Bowen *et al.*, 2013). Most evidence for sympatric speciation in marine fishes comes from studies of incipient species (e.g. Crow, Munehara & Bernardi, 2010).

Two studies using ARC for marine fishes found contrasting results. Quenouille *et al.* (2011) examined wrasses and damselfishes ($N = 18$ sister-species pairs). They found that all sister-species pairs younger than 4 million years were allopatric (seven pairs; 38.9%), but all older pairs were sympatric (11 pairs; 61.1%), implying that the ranges of these older pairs overlapped because of range shifts after allopatric speciation. By contrast, sympatry was dominant within angel-fishes, with no correlation between range overlap and time ($N = 5$ sister-species pairs; Hodge *et al.*, 2013).

(b) Ecological divergence in vertebrates

Studies in many vertebrate groups often find that sister species are ecologically differentiated (e.g. Graham *et al.*, 2004; Funk, Nosil & Etges, 2006; Warren, Glor & Turrelli, 2008). Many well-known cases of ecological speciation in vertebrates involve divergence in diet and/or microhabitat. In granivorous birds, reproductive isolation may be maintained by lower fitness of hybrids with intermediate bill phenotypes (Svensson, 2012). Concurrent divergence in depth and diet is known in freshwater and marine fishes including cichlids, sticklebacks, Arctic char, and rockfish (e.g. Streebman & Danley, 2003; Puebla, 2009; Ingram, 2011; Seehausen & Wagner, 2014).

Many studies have compared climatic data in sister-species pairs, to evaluate if their splitting is potentially explained by climatic-niche divergence or climatic-niche conservatism (i.e. allopatric pairs split by a barrier of climatically unsuitable habitat). For example, Jezkova & Wiens (2018) supported a potential role for climatic-niche divergence in allopatric speciation in ~80% of 49 species pairs of squamate reptiles (lizards and snakes), with niche conservatism supported in the other ~20%. Kozak & Wiens (2006) supported niche conservatism in six out of eight allopatric pairs in salamanders. Thus, both processes can potentially influence

speciation in land vertebrates, and the relative importance of each process may vary from group to group.

Macroevolutionary studies also suggest that climatic-niche divergence may drive speciation in many vertebrate groups, based on increased diversification rates in clades with faster rates of climatic-niche divergence. These include analyses in salamanders (Kozak & Wiens, 2010), frogs (Moen & Wiens, 2017), birds (Cooney, Seddon & Tobias, 2016), and mammals (Castro-Insua *et al.*, 2018). Climatic-niche divergence rates can explain substantial variation in diversification rates among clades in these groups (e.g. salamanders = 41%; frogs = 25%; mammals = 51%). Thus, climatic-niche divergence appears to be important in all major groups of land vertebrates. Nevertheless, more work is needed on the specific processes by which climatic-niche divergence among populations drives speciation and diversification, including within-species patterns of climatic-niche and genetic divergence (e.g. Wang, Glor & Losos, 2013).

The importance of climatic-niche divergence relative to other potential ecological and non-ecological drivers of speciation also remains uncertain. A study in frogs (Moen & Wiens, 2017) found that variation in diversification rates among families was explained by a combination of arboreal microhabitat, rates of climatic-niche evolution, and occurrence in warmer climates, with the first two traits explaining much more variation than the third. Arboreal microhabitat was also important for diversification among squamate families (Bars-Closel *et al.*, 2017), more so than climatic distribution. However, the nature of the connection between this microhabitat and speciation remains uncertain.

Overall, there are dozens (if not hundreds) of studies on how ecological divergence is related to speciation in vertebrates. We suggest that future studies should attempt to address the relative impacts of multiple ecological variables (e.g. diet, microhabitat, climate) on large-scale patterns of diversification and speciation. These can then be coupled with sister-species comparisons of divergence in the same ecological variables, and within-species analyses relating reproductive isolation and/or genetic divergence to divergence in these same traits.

(c) Reproductive isolating barriers in vertebrates

Isolating barriers have been extensively studied in vertebrates, so we provide only a brief summary here. In animals in general, prezygotic barriers are widely believed to be more important for speciation than postzygotic barriers (Ritchie, 2007; Butlin *et al.*, 2012; Seehausen & Wagner, 2014). This inference is often based on the observation that many closely related species are isolated by prezygotic barriers but lack postzygotic barriers. The best-known examples of prezygotic isolating barriers in vertebrates involve ecological differences and behavioural differences between species. In addition to these barriers, mechanical isolation is also known, such as body-size differences that prevent copulation (e.g. Richmond, Jockusch & Latimer, 2011).

Behavioural pre-mating isolation barriers are well studied in birds, and some barriers may be specific to them among

vertebrates. Imprinting on parental phenotypes may be an important factor underlying assortative mating in birds (Randler, 2008; Uy, Irwin & Webster, 2017). Assortative mating for species-specific songs is another hypothesized barrier (Edwards *et al.*, 2005; Uy *et al.*, 2017). In support of this hypothesis, bursts of song divergence and speciation rate increases coincide in some bird radiations (Mason *et al.*, 2017).

Species-specific frog calls are also thought to be important for speciation, based particularly on species-level comparisons (e.g. Hoskin *et al.*, 2005; Boul *et al.*, 2007). However, despite these patterns in birds and frogs, analyses across tetrapods suggest that the presence of acoustic communication in a clade does not increase its diversification rates (Chen & Wiens, 2020).

Intersexual signals that facilitate assortative mating between species are generally thought to be important pre-mating isolating barriers in vertebrates (Streelman & Danley, 2003; Edwards *et al.*, 2005; Maan & Seehausen, 2011; Martin & Mendelson, 2015; Uy *et al.*, 2017). Species-specific visual signals are thought to aid the speciation process and thus explain the high species richness of many groups (Streelman & Danley, 2003). For example, in African cichlids, interspecific hybridization became more common after eutrophication blurred male colour differences (Seehausen, van Alphen & Witte, 1997). However, species-specific visual signals might instead be more important for maintaining reproductive isolation than initiating it. Non-visual sexual signals, such as chemosensory signals, may also help maintain species boundaries in many rodents, squamates, and fishes (Smadja & Butlin, 2009).

Post-mating, prezygotic barriers (including cryptic female choice) are known in vertebrates, but their relative frequency is unclear (Birkhead & Brillard, 2007; Randler, 2008). Evidence for these barriers is perhaps best known in birds, which sometimes have complex female reproductive tracts (Edwards *et al.*, 2005; Birkhead & Brillard, 2007).

The relationship between genetic divergence and hybrid viability has been examined for many vertebrate groups [mammals, birds (Zeh & Zeh, 2000); lizards (Jančúchová-Lásková, Landová & Frynta, 2015); amphibians (Zeh & Zeh, 2000; Malone & Fontenot, 2008); fishes (Bolnick & Near, 2005; Coleman, Harlin-Cognato & Jones, 2009; Stelkens, Young & Seehausen, 2009; Martin & Mendelson, 2015, 2018)]. The rate of formation of postzygotic barriers differs among vertebrate groups. Mammals form these barriers more quickly than other vertebrates (<10 million years; Zeh & Zeh, 2000). By contrast, hybrids have been reported between species separated by >20 million years in all other major vertebrate groups, even up to 100 million years (Jančúchová-Lásková *et al.*, 2015). The faster rate of postzygotic isolation in mammals may be linked to parity. Mammals are almost exclusively viviparous, whereas other vertebrate groups are predominately oviparous (Zeh & Zeh, 2000). Furthermore, viviparous fishes appear to form postzygotic barriers faster than oviparous fishes (Coleman *et al.*, 2009). This pattern is thought to be explained by the greater potential for genomic conflict between mother and

offspring in viviparous taxa. Haldane's rule might also be related to differences in the speed of achieving reproductive isolation. Haldane's rule states that when interspecific hybridization results in sterile offspring for only one sex, it will be the heterogametic sex that is sterile. For example, birds that have heterogametic females (Edwards *et al.*, 2005) may evolve reproductive isolation faster than some fishes that lack distinct sex chromosomes (Bolnick & Near, 2005; Martin & Mendelson, 2018).

VII. MAJOR GENERALIZATIONS AND PATTERNS

The goal of this paper is to compare aspects of speciation across the major groups of living organisms, focusing especially on geographic modes, ecological speciation, and isolating barriers. We also address the frequencies of co-speciation and host-switching. In the preceding sections, we described these aspects in each major group. Here, we make our comparisons across groups for each of these aspects of speciation, starting with co-speciation and host-switching. We also compare diversification rates across groups.

(1) Co-speciation and host-switching

Co-speciation and host-switching are not generally considered fundamental processes in speciation. As one example, these processes are barely mentioned in a classic monograph on speciation (Coyne & Orr, 2004), and did not earn a chapter or section heading.

Based on our results (and on projected species numbers), co-speciation may actually be one of the most numerically important speciation processes (Fig. 1). Our review suggests that endosymbiotic bacteria frequently undergo co-speciation with their insect hosts (~79% of speciation events; Table 1). A recent review (and Section II.2) suggested that each insect species may host around eight unique bacterial endosymbionts, and that most (~70%) species on Earth may be endosymbiotic bacteria (Larsen *et al.*, 2017). Thus, the majority of speciation events on Earth may have involved co-speciation of bacteria and their hosts.

Co-speciation is also widespread in protists and fungi but the relative frequencies of co-speciation and host-switching may be more equal in these groups (Fig. 1). Based on their species-specificity in insect hosts (review in Larsen *et al.*, 2017), the most species-rich groups of protists and fungi may be apicomplexans and microsporidians, respectively. Both co-speciation and host-switching appear to be widespread in apicomplexans, but their frequencies in insect-associated taxa are unclear. Studies of co-speciation and host-switching in insect-associated microsporidians suggest that both processes are present (Shafer *et al.*, 2009; Andreadis *et al.*, 2012). There may also be multiple microsporidian speciation events within a single insect host species (Andreadis *et al.*, 2012). Quantifying the relative frequency of co-speciation and host-switching in these two clades should be

a high priority for understanding speciation generally in protists and fungi.

Animals that are associated with insect hosts may also be critically important for understanding overall patterns of speciation. For example, mite and nematode species may often be associated with a single insect host species, and a single insect species may harbour many mite and nematode species (review in Larsen *et al.*, 2017). Thus, each of these groups may be as (or more) species-rich than insects. Addressing co-speciation and host-switching in insect-associated mites and nematodes may be particularly crucial for estimating the most numerically important speciation processes across animals.

Finally, the exceptional diversity of insects may be associated (at least in part) with interactions with plant hosts. Host-switching may be the key process in this case. We address this below in Section VII.3.

(2) Geographic modes of speciation

Our survey suggests that allopatric speciation might be the most common geographic mode of speciation across the Tree of Life (Fig. 2), based on patterns of range overlap of sister species (see below). However, our review also suggests that there are a few groups in which sympatric speciation might

be as or more common (Fig. 2). For bacteria, there are some potential examples of allopatric speciation, but we caution that insufficient information was available to infer overall frequencies. Similarly, for protists, we have only two relevant species pairs (both allopatric). For fungi, sympatric pairs were slightly more common than allopatric pairs (26 *versus* 24%) and parapatric pairs were also frequent (16%). Interestingly, most sampled pairs were non-specialist pathogens. Allopatric pairs were far more common than sympatric pairs in mushroom-forming Basidiomycota (62 *versus* 12%; $N = 8$; Table S1). In plants, allopatry was most common (30%) but sympatry was similar in frequency (18%), and most species pairs were partially sympatric (52%). Allopatry was clearly more common in animals. Allopatric pairs were most common in molluscs (78%), insects (59%), other marine invertebrates (68%), and vertebrates (53%). However, there were also groups of animals in which sympatric pairs were as or more common than allopatric pairs, including lacustrine (96%) and marine fishes (36%).

Another way to look at the results is in terms of the frequency of fully sympatric sister-species pairs (Fig. 2). We estimated these values for fungi (26%), plants (18%), and various animal groups, including molluscs (15%), insects (23%), marine invertebrates (24%), and vertebrates (10%). Overall, despite the idea that sympatric speciation is more common in

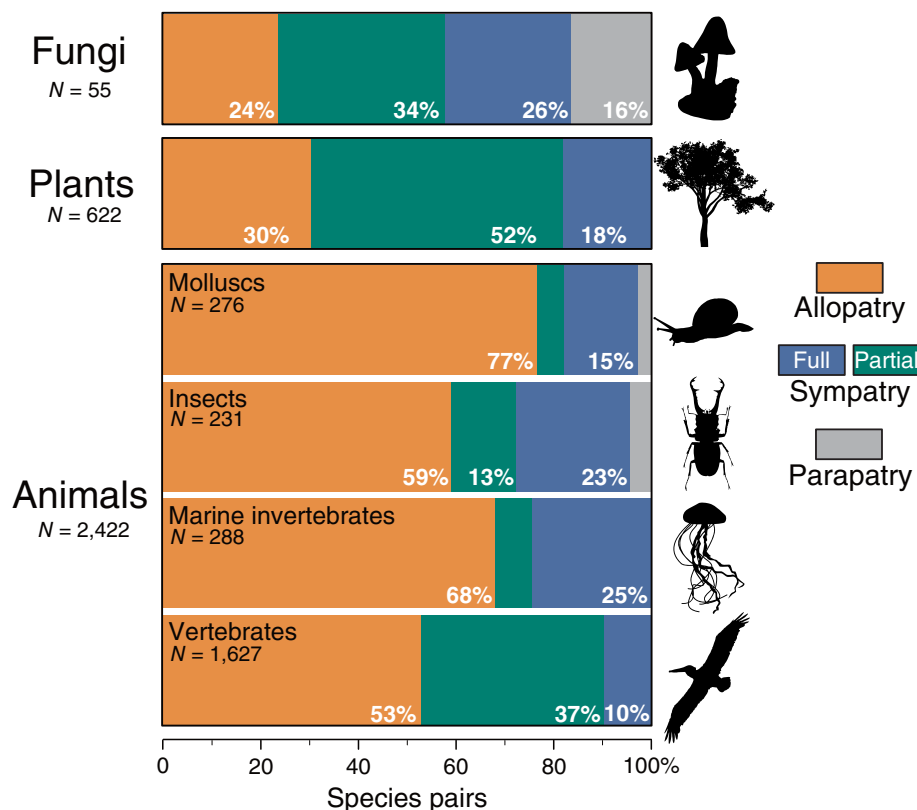


Fig. 2. Relative frequencies of geographic modes of speciation among fungi, plants, and major animal groups. Frequencies are estimated from range overlap of sister-species pairs, which is essential for estimating geographic modes of speciation (Skeels & Cardillo, 2019). Sample size is the number of species pairs for each group. Note that parapatry is treated as partial sympatry in some groups (e.g. plants, vertebrates).

plants than in animals (Stebbins, 1950; Grant, 1981), the frequencies of sympatric species pairs were broadly overlapping between these two groups. Thus, plants had fewer allopatric pairs relative to animals, but similar frequencies of fully sympatric pairs. One potential explanation for this pattern is that allopatric speciation predominates in both groups, but post-speciation dispersal is more common in plants. However, analyses of range overlap over time show negative relationships in plants (Anacker & Strauss, 2014), not the positive relationship expected given allopatry and dispersal.

Another question is whether frequencies of allopatric and sympatric species pairs differ among habitats (i.e. terrestrial, marine, freshwater). This question may be crucial for explaining high marine species richness despite few barriers to dispersal (Bowen *et al.*, 2013), and high freshwater diversity given the limited volume of fresh water (E.C. Miller, in preparation). We focus on molluscs, other (mostly) marine invertebrate phyla, and vertebrates for this comparison, given the few marine plants or fungi (and limited data for protists and bacteria). In molluscs, the frequencies of allopatric *versus* sympatric pairs are broadly similar among marine, freshwater, and terrestrial habitats (76, 73, and 85% allopatric *versus* 15, 20, and 12% sympatric, respectively). For vertebrates, frequencies were ~53% allopatric *versus* ~11% sympatric, dominated by terrestrial species. Allopatry was also dominant among riverine fishes (50 *versus* 13% in sympatry). By contrast, almost all lacustrine fish pairs were sympatric (96%) and marine fish had a higher frequency of sympatric pairs than allopatric pairs (36 *versus* 23%; Table 7). Marine invertebrates (excluding molluscs and arthropods) were similar to terrestrial groups (68% allopatric, 24% sympatric), but with a higher frequency of sympatry, especially in some cnidarians (34% sympatric overall, with 41% in anthozoans and 67% in myxozoans). Among secondarily freshwater lineages of Porifera and Cnidaria (Table 6), geographic patterns were similar to their marine relatives (59% allopatric, 29% sympatric). In insects (mostly terrestrial), fully sympatric sister pairs based on current range overlap were not rare (23%; Table 4), but analyses of overlap over time suggest that this pattern might arise from range shifts (85% allopatry) not sympatric speciation (ARC estimate of sympatry = 14%). Overall, these results do not show strong differences between terrestrial, marine and freshwater habitats, but some groups might have high frequencies of sympatric speciation (e.g. marine and lacustrine fishes). Future studies should use phylogenies to test whether there is a higher frequency of secondary sympatry in the ocean, where barriers to dispersal seem limited.

In summary, our results from range-overlap data suggest that allopatry might be the most common geographic mode across most taxa and habitats (but note that frequencies are unclear for bacteria and protists). At the same time, most groups show a non-trivial number of fully sympatric pairs (10% or higher), and these may outnumber allopatric pairs in fungi and some marine clades. Although these sympatric pairs will require more evidence to establish whether they originated through sympatric speciation, our results are

potentially consistent with the idea that sympatric speciation might explain many speciation events in most groups (despite generally being in the minority).

Finally, we emphasize that all of these inferences are based primarily on range overlap of sister species. This approach has the potential to be accurate, based on simulations (Skeels & Cardillo, 2019), but accuracy is not guaranteed for any given species pair. We emphasize again that sympatric pairs may require additional evidence to support sympatric speciation. At the same time, we are skeptical of the idea that most allopatric sister pairs with currently non-overlapping ranges actually originated in parapatry or sympatry.

(3) Ecological divergence and speciation

Our review suggests that ecological divergence (and possibly speciation) is widespread across the Tree of Life. We found that the most predominant types of ecological divergence fall largely into two main categories: species interactions and abiotic habitat divergence. As described above, species interactions may be critically important for the majority of speciation events across the Tree of Life. First, most living species (~70%) may be endosymbiotic bacteria, and co-speciation between these bacteria and their hosts appears to drive the majority of speciation events in bacteria (~79%; Table 1, Fig. 1). These co-speciation events clearly involve species interactions, but not necessarily ecological divergence. Host-switching is also widespread in endosymbiotic bacteria. Protists and fungi also include many parasitic and symbiotic taxa (especially considering projected species numbers). In these groups, both co-speciation and host-switching appear to drive speciation, possibly at similar frequencies (Fig. 1).

Most living described species are animals, and most of these are insects (~62%; Scholl & Wiens, 2016). Our review suggests that ecological divergence is common among sister species of insects (~80% of 111 pairs) and many of these cases (74% of 65) involved host-plant shifts in herbivorous insects. Intriguingly, these host shifts were more common in allopatric pairs than sympatric pairs (87% *versus* 58%). There is also macroevolutionary evidence that herbivory drives increased diversification rates in insects (e.g. Mitter, Farrell & Wiegmann, 1988; Wiens *et al.*, 2015).

Two-thirds or more of projected animal diversity may consist of mites and nematodes associated with insect hosts (Larsen *et al.*, 2017), and studies are needed to assess whether their speciation typically involves co-speciation, host shifts, or other processes. The role of species interactions in speciation in other animal groups (e.g. vertebrates, molluscs) may be more limited, despite some well-known examples (e.g. diet in birds).

Ecological speciation through species interactions might also be important in plants. Pollinator shifts are considered to be a major driver of ecological speciation in angiosperms (Givnish, 2010), which make up ~90% of land-plant species. There is also macroevolutionary evidence that biotic pollination drove rapid angiosperm diversification (e.g. Hernández-Hernández & Wiens, 2020), but similar studies are needed

for pollinator shifts. Moreover, the actual frequency with which pollinator shifts lead to new species (relative to other processes) remains uncertain. Analyses in Cape Region plants suggest that pollinator divergence is roughly as common as habitat divergence (van der Niet & Johnson, 2009), but whether divergence in these traits actually drives speciation remains uncertain.

Divergence in abiotic habitat may be a second major driver of ecological speciation across the Tree of Life, based on divergence between sister species. However, the relevant aspects of habitat differ across groups. In bacteria, different soil types may be important. In marine protists, divergence in salinity, oxygen content, pH, and nutrients might all drive ecological speciation. In fungi, temperature may be particularly relevant. Quantitative analyses show that habitat divergence is frequent in plants. Similarly, marine invertebrates show habitat divergence that is possibly associated with ecological speciation, including depth and temperature. In terrestrial vertebrates, divergence in climatic niches has been shown to be significant in every major group, based on climatic-niche divergence between sister species and/or correlations between rates of climatic-niche change and diversification (speciation minus extinction).

Finally, our review provides some potential insights on how common ecological speciation may be. For example, two studies in plants spanning hundreds of species suggest that ecological divergence is associated with speciation in about 65–80% of speciation events. In insects, our review suggests the presence of ecological divergence in 80% of 111 species pairs. In molluscs, ecological divergence was reported in 62% of sampled marine pairs and 30% of freshwater pairs. In vertebrates, analyses in squamates suggest that climatic-niche divergence accompanies allopatric speciation in 80% of species. Overall, these patterns suggest that ecological divergence might help explain many speciation events in both plants and animals. This might also be true in free-living bacteria, fungi, and protists, but quantitative analyses are generally lacking.

Nevertheless, a crucial caveat here is that many of these inferences are based on reported ecological differences between sister species. Therefore, it is possible that these ecological differences did not actually drive speciation. Thus, the frequency of ecological speciation may be overestimated. At the same time, it is difficult to conclude that species pairs completely lack ecological differences, unless all possible niche axes have been examined. Thus, ecological speciation could also be underestimated from this approach.

It is also important to note that ecological divergence between sister species is not universal or inevitable. For example, a study in squamate reptiles (Jezkova & Wiens, 2018) suggested that climatic niche conservatism drives allopatric splitting in ~20% of the sampled species pairs, based on analyses showing the separation of allopatric species pairs by a barrier of climatically unsuitable habitat. Similarly, we found possible non-ecological speciation in 20% of 111 sister pairs of insects, most commonly in allopatric pairs. We found no reported evidence for ecological divergence in most

(~75%) species pairs of freshwater molluscs, which are mostly allopatric. Moreover, it is not inevitable that macroevolutionary studies find significant relationships between diversification rates and rates of climatic niche change, or other ecological variables thought to drive speciation based on divergence between sister species.

The strongest evidence for ecological speciation may come from combining these inferences from species pairs with intraspecific results (e.g. strong genetic divergence among individuals in different habitats) and macroevolutionary patterns (e.g. increased diversification rates associated with increased rates of climatic-niche divergence). Another crucial approach is to test directly for positive correlations between reproductive isolation and ecological divergence among species. For example, Funk *et al.* (2006) found that reproductive isolation was significantly related to habitat divergence among eight clades of animals and plants. Similar patterns (but using genetic divergence) were found in bacteria (Vos, 2011).

Along these lines, we emphasize several areas of agreement among different approaches to ecological speciation. For plants, 33% of the 188 sampled species pairs from the Cape Region were found to differ in pollinator types (van der Niet & Johnson, 2009). In macroevolutionary studies across land plants, biotic pollination was the most important driver of increased diversification rates (Hernández-Hernández & Wiens, 2020). Plant sister-species pairs also often occur in different habitats (van der Niet & Johnson, 2009; Anacker & Strauss, 2014), which can differ in climate. Congruently, faster rates of climatic-niche evolution appear to drive faster diversification rates in at least some plant groups (Schnitzler *et al.*, 2012). In insects, we found that among the 111 species pairs with relevant data, ecological divergence was supported in 89 pairs (80%) and many of these (48 pairs) involved host shifts in herbivorous species. At the within-species level, Forbes *et al.* (2017) found widespread evidence for host-associated genetic structure in herbivorous insects. At the macroevolutionary level, the presence of herbivory also explains ~30% of the variation in diversification rates among insect orders (Wiens *et al.*, 2015), and host shifts appear to help drive diversification within herbivorous insect clades (Hardy & Otto, 2014). In land vertebrates, both comparisons of sister species and macroevolutionary studies are consistent with the idea that climatic-niche divergence may often drive speciation. However, more large-scale surveys are also needed to address how often within-species genetic isolation is driven by climatic divergence and not by geographic distance (e.g. Wang *et al.*, 2013). In summary, these patterns of congruence suggest that the observed ecological differences between species pairs in these traits in these groups may be important in driving speciation, and are not simply differences that arise after speciation caused by other factors.

(4) Reproductive isolating barriers

Making comparisons and generalizations about the evolution of isolating barriers was especially difficult. Information was

often patchy, and not standardized among groups. Nevertheless, some interesting observations do emerge.

First, as described above, ecological divergence between species appears to be widespread across the Tree of Life. This appears to be true in bacteria, protists, fungi, plants, and most animal groups. In many cases, this can be considered pre-mating and prezygotic, since individuals in different habitats (or hosts) may never meet.

Second, postzygotic isolation generally seems to be more important than postzygotic isolation across the Tree of Life. For example, in plants, pre-pollination barriers seem typically to contribute more to reproductive isolation than postzygotic barriers (Lowry *et al.*, 2008; Baack *et al.*, 2015). In insects, most of the species surveyed have both prezygotic and postzygotic isolation (79% of 53 pairs), whereas 21% have prezygotic but not postzygotic isolation. This pattern suggests that prezygotic isolation evolves first (Coyne & Orr, 1989, 1997). In vertebrates, prezygotic barriers are believed to be more important than postzygotic barriers. Furthermore, postzygotic barriers appear to form relatively slowly in vertebrates, much slower than the rate of species formation (e.g. Stelkens *et al.*, 2009). In marine invertebrates, many species use broadcast spawning and species are isolated prezygotically by the timing of gamete release and by gametic incompatibility. Gametic incompatibility appears to be widespread in protists. In fungi, strong pre-mating isolation is present in some groups, although the relationship to postzygotic isolation is unclear. Bacteria do not form gametes (or zygotes), but recombination between species is only possible between similar sequences. Nevertheless, postzygotic isolation is also present in many groups, including animals and plants.

Third, hybrid and polyploid speciation are widespread across the Tree of Life (if not necessarily common). For example, hybrid speciation is hypothesized in fungi, plants, and some animals (e.g. cnidarians). However, detecting hybrid speciation is controversial (e.g. Schumer, Rosenthal & Andolfatto, 2014; Feliner *et al.*, 2017), and this debate impacts how common this process is inferred to be. Speciation through polyploidy occurs in many protist taxa and may account for ~15% of speciation events in plants. Polyploid speciation is generally considered to be rare in animals, and this difference with plants is a subject of considerable debate (Coyne & Orr, 2004).

(5) Rates of diversification and speciation

One quantitative aspect of speciation that has been compared across groups is the rate (e.g. Coyne & Orr, 2004). The rate of diversification (speciation minus extinction) is relatively straightforward to estimate with only the ages of clades and their richness. However, extracting a speciation rate from this information is challenging. Here, we assume that variation in diversification rates is positively related to variation in speciation rates (as is widely done; Coyne & Orr, 2004). We briefly review a set of diversification rate estimates for the major groups addressed herein, in which all

estimates should be directly comparable (the only such set of estimates we are aware of). These estimates (from Scholl & Wiens, 2016) were all based on the method-of-moments estimator for stem groups (Magallón & Sanderson, 2001), using an intermediate epsilon value (0.5; alternative values have limited impact on relative rates among groups). Simulations show that this estimator is relatively accurate, and can be robust to variation in rates within clades over time and between subclades (Meyer, Román-Palacios & Wiens, 2018) and to faster rates in younger clades (Kozak & Wiens, 2016). It is also straightforward to examine the impact of changing species numbers within clades using this approach.

Among major clades, land plants have relatively rapid diversification rates [0.0278 species per million years (Myr)] relative to animals (0.0141) and fungi (0.0085). The high rate in plants is almost certainly driven by angiosperms (which contain 90% of land plants, rate = 0.0332). Major clades of protists are slower (e.g. Amoebozoa = 0.0040; Excavata = 0.0034; SAR clade = 0.0062). The slowest rates are in bacteria (0.0020) and archaeans (0.0014).

These estimates are based on numbers of described species. If projected bacterial richness is used (e.g. ~1 billion species; Larsen *et al.*, 2017), the rate is higher, but similar in magnitude (0.0048). Projections of bacterial richness that are ten times lower or higher than 1 billion yield similar rate estimates (0.0042, 0.0054). These rate estimates are low because bacteria are extremely old. Similarly, assuming high species richness for animals (163 million; Larsen *et al.*, 2017) yields a similar rate (0.0190). Of course, there is important variation within these major clades. However, rates for subclades do tend to be correlated with those of their major clades (Scholl & Wiens, 2016).

Overall, there seem to be striking differences in speciation rates across the Tree of Life (based on variation in diversification rates). A major challenge for future studies is to determine whether these differences in rates are related to differences in processes of speciation. Intriguingly, our review does not suggest any obvious differences that would explain the variation in rates. There is a large literature linking variation in diversification rates to specific traits (review in Wiens, 2017), such as herbivory in insects (e.g. Mitter *et al.*, 1988; Wiens *et al.*, 2015), biotic pollination in plants (e.g. Bruun-Lund *et al.*, 2018; Hernández-Hernández & Wiens, 2020), and climatic-niche change and microhabitat in vertebrates (see Section VII.3). Nevertheless, we do have some examples where it is possible to link these large-scale relationships to patterns at the species level (e.g. insect herbivory, angiosperm pollination, vertebrate climatic niches).

VIII. CONCLUSIONS

- (1) Synthetic studies of speciation tend to focus on particular topics or particular taxa. Here we attempted to look for differences and generalities in speciation among major groups across the Tree of Life.

- (2) The most numerically frequent speciation process across the Tree of Life may be co-speciation between endosymbiotic bacteria and their insect hosts, given estimates that ~70% of projected species may be host-associated bacteria and given our estimate that ~79% of sampled nodes show a pattern consistent with co-speciation. We also suggest that recent claims of very limited bacterial diversity associated with animal hosts are almost certainly incorrect.
- (3) Allopatric speciation (inferred from allopatry of sister species) seems to be present in all major groups, and may be the most frequent mode in both animals and plants. Full sympatry of sister species is also widespread (consistent with sympatric speciation), and appears to be more frequent in fungi than allopatry. Sympatric sister species are more common in some marine animal groups (e.g. some cnidarians, fishes) and in lacustrine fishes than in terrestrial, freshwater, or marine animals in general.
- (4) Ecological divergence (essential for ecological speciation) is widespread in all groups, including ~70% of species pairs of plants and insects surveyed here. Across the Tree of Life, ecological divergence typically involves either species interactions (e.g. host-switching) or habitat divergence. More work is needed to confirm that these cases of ecological divergence between sister species do indeed represent ecological speciation. Nevertheless, inferences from species pairs are supported by macroevolutionary analyses of diversification rates for some key ecological traits (e.g. insect herbivory, plant pollination, climatic niche divergence).
- (5) Prezygotic isolation may be generally more widespread and important than postzygotic isolation. For example, postzygotic isolation seems to lag behind speciation in insects and vertebrates, although not in plants. However, many species are isolated by both prezygotic and postzygotic barriers (e.g. in insects and plants). Ecological divergence and gametic incompatibility are widespread prezygotic barriers in many groups, with gametic incompatibility documented in protists, insects, and marine invertebrates, and ecological divergence in almost all groups.
- (6) Rates of diversification (and presumably speciation) are strikingly different among major clades across the Tree of Life, with rates in plants twice as fast as those in animals, more rapid rates in animals than in fungi, and the slowest rates in protists and prokaryotes.

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XI. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Appendix S1. Methods for literature searches.
Appendix S2. Supplementary Tables S1–S10.

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