Speciation across the Tree of Life

Tania Hernández-Hernández[1,2†], Elizabeth C. Miller[1†], Cristian Román-Palacios[1†] and John J. Wiens[1†]* 🔘

[1]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, 85721-0088, U.S.A.*
[2]*Catedrática CONACYT asignada a LANGEBIO-UGA Cinvestav, Libramiento Norte Carretera León Km 9.6, 36821, Irapuato, Guanajuato, Mexico*

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

---

* Address for correspondence (Tel: +520 621 0337; E-mail: wiensj@email.arizona.edu)
† Order of authorship is alphabetical.

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 archaean. 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. Carrolo *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 endosymbiotes (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 (Seears, Darling & Wade, 2012). Wylezich *et al.* (2012) suggested that

Table 1. Summary of congruent and incongruent nodes in comparisons of phylogenetic trees between bacterial symbiotes 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 *et al.* (2009)
Nycteribiid flies	6/7 (86%)	1/7	0/7	Hosokawa *et al.* (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 *et al.* (1998)
Glossinidae (tsetse flies)	5/5 (100%)	0/5	0/6	Chen *et al.* (1999)
Aphids (genus *Uroleucon*)	5/8 (62%)	2/8	1/8	Clark *et al.* (2000)
Dryophthorid beetles	7/10 (70%)	3/10	0/10	Lefevre *et al.* (2004)
Carpenter ants	6/12 (50%)	3/12	3/12	Sauer *et al.* (2000)
Psyllid plant lice (Hemiptera)	9/9 (100%)	0/9	0/9	Thao *et al.* (2000)
Plataspid stinkbugs	7/7 (100%)	0/7	0/7	Hosokawa *et al.* (2006)
Aphids (multiple genera)	9/9 (100%)	0/9	0/9	Moran *et al.* (1993)
Cockroaches	8/9 (89%)	1/9	0/9	Lo *et al.* (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 *Crypthecodinium cohnii* species complex (Dinozoa), 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 though gametic incompatibility has been reported in many other diatoms (1 sister pair: Chromalveolata: *Pseudo-nitzschia*; 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
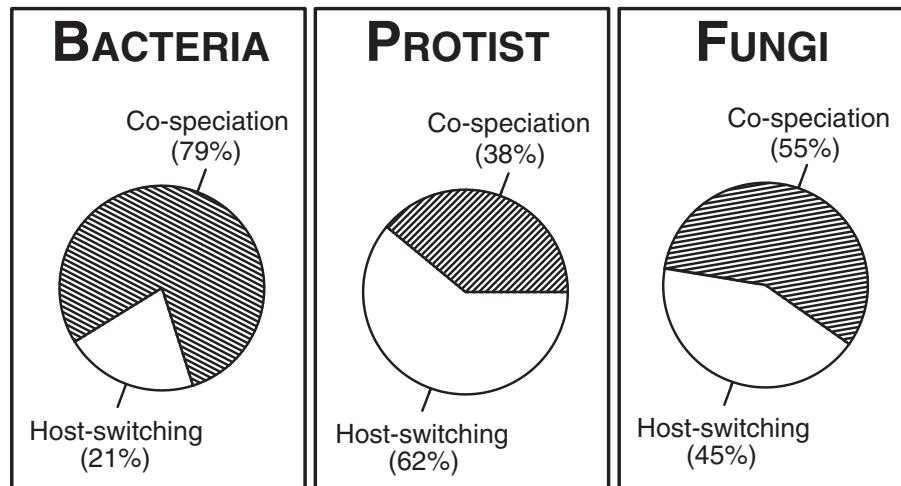
Fig. 1. Relative frequencies of co-speciation and host-switching in symbiotic bacteria, protists, and fungi. Values for bacteria are based on Table 1 (mean across studies), with a total sample size of 103 speciation events. Values for protists are based on the overall frequency of modes across all reported 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, 'phylospecies' were isolated by habitat characteristics, notably temperature. Phylospecies 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 & Gavrilets, 2010). However, studies often identify cryptic phylospecies 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*, phylospecies 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 phylospecies 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 *Epichloë* (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 pseudotritici* 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 *et al.* (2007)
Piper subgenus *Ottonia* (Piperaceae), 9 sister pairs	Atlantic forest of Brazil, Amazon and west Andes	22.2% allopatric, 0% sympatric, 77.8% partially sympatric*	Molina-Henao *et al.* (2016)
Primulaceae, 11 sister pairs	Mountains of the European alpine system	45.4% allopatric, 0% sympatric, 54.5% partially sympatric	Boucher *et al.* (2016)
Costus (Costaceae), 54 sister pairs	Neotropics	18.5% allopatric, 38.9% sympatric, 42.6% partially sympatric*	André *et al.* (2016)
Mimulus (Phrymaceae), 24 sister pairs	North America	20.8% allopatric, 37.5% sympatric, 41.7% partially sympatric	Grossenbacher *et al.* (2014)
Angiosperms, 52 sister pairs	Hawaiian Islands	28.8% allopatric 42.3% sympatric, 28.8% parapatric (adjacent but non-overlapping)	Price & Wagner (2004)
Banksia, *Hakea*, *Protea* (Proteaceae), 122 sister pairs	Australia, South Africa	35.7% allopatric, 23.6% sympatric, 40.8% partially sympatric	Skeels & Cardillo (2019)
Sidalcea (Malvaceae), 8 sister pairs	North America	25.0% allopatric, 37.5% sympatric, 37.5% partially sympatric	Skeels & Cardillo (2019)
Bursera (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 F_2 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, *Acyrthosiphon* 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 (Carlon *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 congenerics, 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); Phillimore *et al.* (2008); Skeels & Cardillo (2019)
Amphibians	190	106 (55.8%)	60 (31.6%)	24 (12.6%)	Kozak & Wiens (2006); Hua & Wiens (2010); Wollenberg *et al.* (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 *et al.* (2011); Hodge *et al.* (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 angelfishes, 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. Streelman & 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 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 premating 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
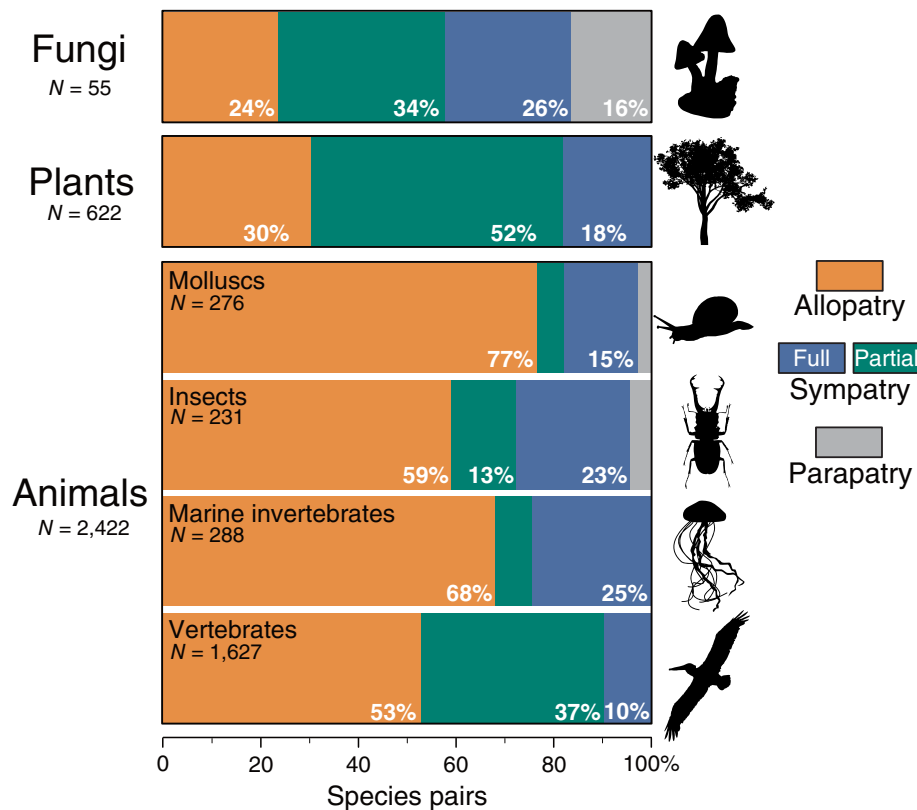

Fig. 2. Relative frequencies of geographic modes of speciation among fungi, plants, and major animal groups. Frequencies are estimated from range overlap of sister-species pairs, which is essential for estimating geographic modes of speciation (Skeels & Cardillo, 2019). Sample size is the number of species 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, prezygotic 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.

IX. ACKNOWLEDGEMENTS

X. REFERENCES

References identified with an asterisk (*) are cited only in the Supporting Information.*

ABBOT, P. & WITHGOTT, J. H. (2004). Phylogenetic and molecular evidence for allochronic speciation in gall-forming aphids (*Pemphigus*). *Evolution* **58**, 539–553.

ABBOTT, R., ALBACH, D., ANSELL, S., ARNTZEN, J., BAIRD, S. J. E., BIERNE, J., BOUGHMAN, J., BRELSFORD, A., BUERKLE, C. A., BUGGS, R., BUTLIN, R. K., DIECKMANN, U., EROUKHMANOFF, F., GRILL, A., CAHAN, S. H., et al. (2013). Hybridization and speciation. *Journal of Evolutionary Biology* **26**, 229–246.

*ABRAHAMSON, W. G., EUBANKS, M. D., BLAIR, C. P. & WHIPPLE, A. V. (2001). Gall flies, inquilines, and goldenrods: a model for host-race formation and sympatric speciation. *American Zoologist* **41**, 928–938.

*ADL, S. M., LEANDER, B. S., SIMPSON, A. G. B., ARCHIBALD, J. M., ANDERSON, O. R., BASS, D., BOSWER, S. S., BRUGEROLLE, G., FARMER, M. A., KARPOV, S., KOLISKO, M., LANE, C. E., LODGE, D. J., MANN, D. G., MEISTERFELD, R., et al. (2007). Diversity, nomenclature, and taxonomy of protists. *Systematic Biology* **56**, 684–689.

*ALBERTINI, C., THEBAUD, G., FOURNIER, E. & LEROUX, P. (2002). Eburicol 14a-demethylase gene (*CYP51*) polymorphism and speciation in *Botrytis cinerea*. *Mycological Research* **106**, 1171–1178.

*ALDROVANDI, M. S. P., JOHNSON, J. E., O'MEARA, B., PETERSEN, R. H. & HUGHES, K. W. (2015). The *Xeromphalina campanella/kauffmanii* complex: species delineation and biogeographical patterns of speciation. *Mycologia* **107**, 1270–1284.

*ALIPAZ, J. A., WU, C. & KARR, T. L. (2001). Gametic incompatibilities between races of *Drosophila melanogaster*. *Proceedings of the Royal Society of London B: Biological Sciences* **268**, 789–795.

*ALTHOFF, D. M. (2014). Shift in egg-laying strategy to avoid plant defense leads to reproductive isolation in mutualistic and cheating yucca moths. *Evolution* **68**, 301–307.

*ALTHOFF, D. M., SEGRAVES, K. A., SMITH, C. I., LEEBENS-MACK, J. & PELLMYR, O. (2012). Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification. *Molecular Phylogenetics and Evolution* **62**, 898–906.

AMATO, A., KOOISTRA, W. H. C. F., LEVIALDI GHIRON, J. H., MANN, D. G., PRÖSCHOLD, T. & MONTRESOR, M. (2007). Reproductive isolation among sympatric cryptic species in marine diatoms. *Protist* **158**, 193–207.

*AMOR, M. D., NORMAN, M. D., CAMERON, H. E. & STRUGNELL, J. M. (2014). Allopatric speciation within a cryptic species complex of Australasian octopuses. *PLoS One* **9**, 1–13.

ANACKER, B. L. & STRAUSS, S. Y. (2014). The geography and ecology of plant speciation: range overlap and niche divergence in sister species. *Proceedings of the Royal Society of London B: Biological Sciences* **281**, 20132980.

ANDRÉ, T., SALZMAN, S., WENDT, T. & SPECHT, C. D. (2016). Speciation dynamics and biogeography of Neotropical spiral gingers (Costaceae). *Molecular Phylogenetics and Evolution* **103**, 55–63.

ANDREADIS, T. G., SIMAKOVA, A. V., VOSSBRINCK, C. R., SHEPARD, J. J. & YURCHENKO, Y. A. (2012). Ultrastructural characterization and comparative phylogenetic analysis of new microsporidia from Siberian mosquitoes: evidence for coevolution and host switching. *Journal of Invertebrate Pathology* **109**, 59–75.

*ANDREAKIS, N., LUTER, H. M. & WEBSTER, N. S. (2012). Cryptic speciation and phylogeographic relationships in the elephant ear sponge *Ianthella basta* (Porifera, Ianthellidae) from northern Australia. *Zoological Journal of the Linnaean Society London*. **166**, 225–235.

*ANDRÉS, J. A., MAROJA, L. S., BOGDANOWICZ, S. M., SWANSON, W. J. & HARRISON, R. G. (2006). Molecular evolution of seminal proteins in field crickets. *Molecular Biology and Evolution* **23**, 1574–1584.

APPELTANS, W., AHYONG, S. T., ANDERSON, G., ANGEL, M. V., ARTOIS, T., BAILLY, N., BAMBER, R., BARBER, A., BARTSCH, I., BERTA, A., BLAZEWICZ-PASZOWYCZ, M., BOCK, P., BOXSHALL, G., BOYKO, C. B., BRANDAO, S. N., et al. (2012). The magnitude of global marine species diversity. *Current Biology* **22**, 2189–2202.

*ARAUJO, R., BUCKLEY, D., NAGEL, K.-O. & MACHOROM, A. (2016). *Potomida littoralis* (Bivalvia, Unionidae) evolutionary history: slow evolution or recent speciation? *Zoological Journal of the Linnean Society*. https://doi.org/10.1111/zoj.12470.

*ARBUTHNOTT, D. & CRESPI, B. J. (2009). Courtship and mate discrimination within and between species of *Timema* walking-sticks. *Animal Behaviour* **78**, 53–59.

*ARBUTHNOTT, D., ELLIOT, M. G., McPEEK, M. A. & CRESPI, B. J. (2010). Divergent patterns of diversification in courtship and genitalic characters of *Timema* walking-sticks. *Journal of Evolutionary Biology* **23**, 1399–1411.

ARNQVIST, G., EDVARDSSON, M., FRIBERG, U. & NILSSON, T. (2000). Sexual conflict promotes speciation in insects. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 10460–10464.

AURY, J. M., JAILLON, O., DURET, L., NOEL, B., JUBIN, C., PORCEL, B. M., SÉGURENS, B., DAUBIN, V., ANTHOUARD, V., AIACH, N., ARNAIZ, O., BILLAUT, A., BEISSO, I., BLANC, I., BOUHOUCHE, K., et al. (2006). Global trends of whole-genome duplications revealed by the ciliate *Paramecium tetraurelia*. *Nature* **444**, 171–178.

*Ayala, F. J., Tracey, M. L., Barr, L. G. & Ehrenfeld, J. G. (1974). Genetic and reproductive differentiation of the subspecies, *Drosophila equinoxialis caribbensis*. *Evolution* 28, 24–41.

Baack, E., Melo, M. C., Rieseberg, L. H. & Ortiz-Barrientos, D. (2015). The origins of reproductive isolation in plants. *New Phytologist* 207, 968–984.

Baas Becking, L. G. M. (1934). *Geobiologie of inleiding tot de milieukunde.* W.P. Van Stockum & Zoon, Den Haag.

Barraclough, T. G. (2019). *The Evolutionary Biology of Species.* Oxford University Press, Oxford.

*Barraclough, T. G., Fontaneto, D., Hernique, E. & Ricci, C. (2009). The evolutionary nature of diversification in sexuals and asexuals. In *Speciation and Patterns of Diversity* (eds R. Butlin, J. Bridle and D. Schluter), pp. 29–45. Ecological Reviews, Cambridge.

Barraclough, T. G. & Vogler, A. P. (2000). Detecting the geographical pattern of speciation from species-level phylogenies. *American Naturalist* 155, 419–434.

Bars-Closel, M., Kohlsdorf, T., Moen, D. S. & Wiens, J. J. (2017). Diversification rates are more strongly related to microhabitat than climate in squamate reptiles (lizards and snakes). *Evolution* 71, 2243–2261.

*Bartošová-Sojková, P., Hrabcová, M., Pecková, H., Patra, S., Kodádková, A., Jurajda, P., Tyml, T. & Holzer, A. S. (2014). Hidden diversity and evolutionary trends in malacosporean parasites (Cnidaria: Myxozoa) identified using molecular phylogenetics. *International Journal for Parasitology* 44, 565–577.

Bass, D. & Boenigk, J. (2011). Everything is everywhere: a twenty-first century de−/reconstruction with respect to protists. *Biogeography of Microscopic Organisms* 6, 88–110.

Beam, C. A. & Himes, M. (1977). Sexual isolation and genetic diversification among some strains of *Crypthecodinium cohnii*-like dinoflagellates evidence of speciation. *The Journal of Protozoology* 24, 532–539.

Beijerinck, M. W. (1913). *De infusies en de ontdekking der backterien. Jaarboek van de Koninklijke Akademie voor Wetenschappen.* Müller, Amsterdam.

*Bell, G. (2009). The poverty of the protists. In *Speciation and Patterns of Diversity* (eds R. Butlin, J. Bridle and D. Schluter), pp. 46–58. Ecological Reviews, Cambridge.

*Bell, K. L., Moritz, C., Moussalli, A. & Yeates, D. K. (2007). Comparative phylogeography and speciation of dung beetles from the Australian wet tropics rainforest. *Molecular Ecology* 16, 4984–4998.

*Bendall, E. E., Vertacnik, K. L. & Linnen, C. R. (2017). Oviposition traits generate extrinsic postzygotic isolation between two pine sawfly species. *BMC Evolutionary Biology* 17, 26.

Bendall, M. L., Stevens, S. L., Chan, L.-K., Malfatti, S., Schwientek, P., Tremblay, J., Schackwitz, W., Martin, J., Pati, A., Bushnell, B., Froula, J., Kang, D., Tringe, S. G., Bertilsson, S., Moran, M. A., Shade, A., Newton, R. J., McMahon, K. D. & Malmstrom, R. R. (2016). Genome-wide selective sweeps and gene-specific sweeps in natural bacterial populations revealed by time-series metagenomics. *ISME Journal* 10, 1589–1601.

*Bentlage, B., Cartwright, P., Yanagihara, A. A., Lewis, C., Richards, G. S. & Collins, A. G. (2009). Evolution of box jellyfish (Cnidaria: Cubozoa), a group of highly toxic invertebrates. *Proceedings of the Royal Society of London B: Biological Sciences* 277, 493–501.

*Berlocher, S. H. (2000). Radiation and divergence in the *Rhagoletis pomonella* species group: inferences from allozymes. *Evolution* 54, 543–557.

*Berlocher, S. H. (2003). When houseguests become parasites: sympatric speciation in ants. *Proceedings of the National Academy of Sciences of the United States of America* 100, 6896–6898.

Berlocher, S. H. & Feder, J. L. (2002). Sympatric speciation in phytophagous insects: moving beyond controversy? *Annual Review of Entomology* 47, 773–815.

*Bethenod, M.-T., Thomas, Y., Rousset, F., Frerot, B., Pelozuelo, L., Genestier, G. & Bourguet, D. (2005). Genetic isolation between two sympatric host plant races of the European corn borer, *Ostrinia nubilalis* Hubner. II: assortative mating and host-plant preferences for oviposition. *Heredity* 94, 264–270.

Bidochka, M. J., Menzies, F. V. & Kamp, A. M. (2002). Genetic groups of the insect-pathogenic fungus *Beauveria bassiana* are associated with habitat and thermal growth preferences. *Archives of Microbiology* 178, 531–537.

Bidochka, M. J., Small, C. L. N. & Spironello, M. (2005). Recombination within sympatric cryptic species of the insect pathogenic fungus *Metarhizium anisopliae*. *Environmental Microbiology* 7, 1361–1368.

Bierne, N., Bonhomme, F. & David, P. (2003). Habitat preference and the marine-speciation paradox. *Proceedings of the Royal Society B: Biological Sciences* 270, 1399–1406.

*Bierne, N., David, P., Langlade, A. & Bonhomme, F. (2002). Can habitat specialisation maintain a mosaic hybrid zone in marine bivalves? *Marine Ecology Progress Series* 245, 157–170.

Billiard, S., López-Villavicencio, M., Hood, M. E. & Giraud, T. (2012). Sex, outcrossing and mating types: unsolved questions in fungi and beyond. *Journal of Evolutionary Biology* 25, 1020–1038.

Binks, R. M., Prince, J., Evans, J. P. & Kennington, W. J. (2012). More than bindin divergence: reproductive isolation between sympatric subspecies of a sea urchin by asynchronous spawning. *Evolution* 66, 3545–3557.

Bird, C. E., Holland, B. S., Bowen, B. W. & Toonen, R. J. (2011). Diversification of sympatric broadcast-spawning limpets (*Cellana* spp.) within the Hawaiian archipelago. *Molecular Ecology* 20, 2128–2141.

Birkhead, T. R. & Brillard, J. P. (2007). Reproductive isolation in birds: postcopulatory prezygotic barriers. *Trends in Ecology and Evolution* 22, 266–272.

*Blackwell, M. (2011). The Fungi: 1, 2, 3…5.1 million species? *American Journal of Botany* 98, 426–438.

*Blair, C. P., Abrahamson, W. G., Jackman, J. A., Tyrrell, L. & Nason, J. (2005). Cryptic speciation and host-race formation in a purportedly generalist tumbling flower beetle. *Evolution* 59, 304–316.

Blank, R. J. & Trench, R. K. (1985). Speciation and symbiotic dinoflagellates. *Science* 229, 656–658.

*Boake, C. R. B., Andreadis, D. K. & Witzel, A. (2000). Behavioural isolation between two closely related Hawaiian *Drosophila* species: the role of courtship. *Animal Behaviour* 60, 495–501.

Bobay, L.-M. & Ochman, H. (2017). Biological species are universal across life's domains. *Genome Biology and Evolution* 9, 491–501.

*Bock, D. G., MacIsaac, H. J. & Cristescu, M. E. (2012). Multilocus genetic analyses differentiate between widespread and spatially restricted cryptic species in a model ascidian. *Proceedings of the Royal Society of London B: Biological Sciences* 279, 2377–2385.

*Boissin, E., Féral, J. P. & Chenuil, A. (2008). Defining reproductively isolated units in a cryptic and syntopic species complex using mitochondrial and nuclear markers: the brooding brittle star, *Amphipholis squamata* (Ophiuroidea). *Molecular Ecology* 17, 1732–1744.

*Boissin, E., Stöhr, S. & Chenuil, A. (2011). Did vicariance and adaptation drive cryptic speciation and evolution of brooding in *Ophioderma longicauda* (Echinodermata: Ophiuroidea), a common Atlanto-Mediterranean ophiuroid? *Molecular Ecology* 20, 4737–4755.

Bolnick, D. I. & Fitzpatrick, B. M. (2007). Sympatric speciation: models and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics* 38, 459–487.

Bolnick, D. I. & Near, T. J. (2005). Tempo of hybrid inviability in centrarchid fishes (Teleostei: Centrarchidae). *Evolution* 59, 1754–1767.

*Bordenstein, S. R. & Werren, J. H. (1998). Effects of A and B *Wolbachia* and host genotype on interspecies cytoplasmic in- compatibility. *Genetics* 148, 1833–1844.

*Bordenstein, S. R., O'Hara, F. P. & Werren, J. H. (2001). *Wolbachia*-induced incompatibility precedes other hybrid incompatibilities in *Nasonia*. *Nature* 409, 707–710.

*Borrero-Pérez, G. H., Gómez-Zurita, J., González-Wangüemert, M., Marcos, C. & Pérez-Ruzafa, A. (2010). Molecular systematics of the genus *Holothuria* in the Mediterranean and northeastern Atlantic and a molecular clock for the diversification of the Holothuriidae (Echinodermata: Holothuroidea). *Molecular Phylogenetics and Evolution* 57, 899–906.

Boucher, F. C., Zimmermann, N. E. & Conti, E. (2016). Allopatric speciation with little niche divergence is common among alpine Primulaceae. *Journal of Biogeography* 43, 591–602.

Boul, K. E., Funk, W. C., Darst, C. R., Cannatella, D. C. & Ryan, M. J. (2007). Sexual selection drives speciation in an Amazonian frog. *Proceedings of the Royal Society B: Biological Sciences* 274, 399–406.

*Bourke, A. F. G. & Franks, N. R. (1991). Alternative adaptations, sympatric speciation, and the evolution of parasitic, inquiline ants. *Biological Journal of the Linnean Society* 43, 157–178.

*Boury-Esnault, N., Solé-Cava, A. M. & Thorpe, J. P. (1992). Genetic and cytological divergence between colour morphs of the Mediterranean sponge *Oscarella lobularis* Schmidt (Porifera, Demospongiae, Oscarellidae). *Journal of Natural History* 26, 271–284.

*Bouzon, J. L., Vargas, S. M., Oliveira Neto, J. F., Stoco, P. H. & Brandini, F. P. (2014). Cryptic species and genetic structure in *Didemnum granulatum* Tokioka, 1954 (Tunicata: Ascidiacea) from the southern Brazilian coast. *Brazilian Journal of Biology* 74, 923–932.

Bowen, B. W., Rocha, L. A., Toonen, R. J. & Karl, S. A. (2013). The origins of tropical marine biodiversity. *Trends in Ecology and Evolution* 28, 359–366.

*Breeuwer, J. A. J. & Werren, J. H. (1990). Microorganisms associated with chromosome destruction and reproductive isolation between two insect species. *Nature* 346, 558–560.

*Breeuwer, J. A. J. & Werren, J. H. (1995). Hybrid breakdown between two haplodiploid species: the role of nuclear and cytoplasmic genes. *Evolution* 49, 705–717.

*Broughton, R. E. & Harrison, R. G. (2003). Nuclear gene genealogies reveal historical, demographic and selective factors associated with speciation in field crickets. *Genetics* 163, 1389–1401.

*Brown, J. M., Abrahamson, W. G., Packer, R. A. & Way, P. A. (1995). The role of natural-enemy escape in a gallmaker host-plant shift. *Oecologia* 104, 52–60.

Bruns, T. D., Bidartondo, M. I. & Taylor, D. L. (2002). Host specificity in ectomycorrhizal communities: what do the exceptions tell us? *Integrative and Comparative Biology* 42, 352–359.

Bruun-Lund, S., Verstraete, B., Kjellberg, F. & Rønsted, N. (2018). Rush hour at the museum–diversification patterns provide new clues for the success of figs (*Ficus* L., Moraceae). *Acta Oecologica* **90**, 4–11.

Bush, A. M., Hunt, G. & Bambach, R. K. (2016). Sex and the shifting biodiversity dynamics of marine animals in deep time. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 14073–14078.

*Bush, G. L. (1969a). Mating behavior, host specificity, and the ecological significance of sibling species in frugivorous flies of the genus *Rhagoletis* (Diptera-Tephritidae). *American Naturalist* **103**, 669–672.

*Bush, G. L. (1969b). Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera, Tephritidae). *Evolution* **23**, 237–251.

*Butlin, R. K. (1996). Co-ordination of the sexual signaling system and genetic basis of differentiation between populations of the brown planthopper, *Nilaparvata lugens*. *Heredity* **77**, 369–377.

*Butlin, R. K. (1998). What do hybrid zones in general, and the *Chorthippus parallelus* zone in particular, tell us about speciation. In *Endless Forms: Species and Speciation* (eds D. Otte and J. Endler), pp. 367–378. Sinauer Associates, Sunderland.

*Butlin, R. K. & Hewitt, G. M. (1985). A hybrid zone between *Chorthippus parallelus parallelus* and *Chorthippus parallelus erythropus* (Orthoptera: Acrididae): behavioural characters. *Biological Journal of the Linnean Society* **26**, 287–299.

*Butlin, R. K. & Hewitt, G. M. (2008). Genetics of behavioural and morphological differences between parapatric subspecies of *Chorthippus parallelus* (Orthoptera: Acrididae). *Biological Journal of the Linnean Society* **33**, 233–248.

*Butlin, R. K. & Ritchie, M. G. (2002). Variation in female mate preference across a grasshopper hybrid zone. *Journal of Evolutionary Biology* **4**, 227–240.

Butlin, R., Debelle, A., Kerth, C., Snook, R. R., Beukeboom, L. W., Castillo Cajas, R. F., Diao, W., Maan, M. E., Paolucci, S., Weissing, F. J. & van de Zande, L. (2012). What do we need to know about speciation? *Trends in Ecology and Evolution* **27**, 27–39.

*Caillaud, M. C. & Via, S. (2000). Specialized feeding behavior influences both ecological specialization and assortative mating in sympatric host races of pea aphids. *American Naturalist* **156**, 606–621.

*Calcagno, Y., Thomas, Y. & Bourguet, D. (2007). Sympatric host races of the European corn borer: adaptation to host plants and hybrid performance. *Journal of Evolutionary Biology* **20**, 1720–1729.

Cameron, R. A. D. (2013). The diversity of land molluscs - questions unanswered and questions unasked. *American Malacological Bulletin* **31**, 169–180.

*Caputi, L., Andreakis, N., Mastrototaro, F., Cirino, P., Vassillo, M. & Sordino, P. (2007). Cryptic speciation in a model invertebrate chordate. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 9364–9369.

*Carlon, D. B. & Budd, A. F. (2002). Incipient speciation across a depth gradient in a scleractinian coral? *Evolution* **56**, 2227–2242.

Carlon, D. B., Budd, A. F., Lippe, C. & Andrew, R. L. (2011). The quantitative genetics of incipient speciation: heritability and genetic correlations of skeletal traits in populations of diverging *Favia fragum* ecomorphs. *Evolution* **65**, 3428–3447.

*Carroll, S. P., Dingle, H., Famula, T. R. & Fox, C. W. (2001). Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. In *Microevolution Rate, Pattern, Process. Contemporary Issues in Genetics and Evolution* (Volume **8**, eds A. P. Hendry and M. T. Kinnison). Springer, Dordrecht.

Carrolo, M., Pinto, F. R., Melo-Cristino, J. & Ramirez, M. (2009). Phenotypes are driving genetic differentiation within *Streptococcus pneumoniae*. *BMC Microbiology* **9**, 191.

*Cassone, B. J., Mouline, K., Hahn, M. W., White, B. J., Pombi, M., Simard, F., Constantini, C. & Besansky, N. J. (2008). Differential gene expression in incipient species of *Anopheles gambiae*. *Molecular Ecology* **17**, 2491–2504.

Castro-Insua, A., Gómez-Rodríguez, C., Wiens, J. J. & Baselga, A. (2018). Climatic niche divergence drives patterns of diversification and richness among mammal families. *Scientific Reports* **8**, 8781.

Chae, E., Bomblies, K., Kim, S. T., Karelina, D., Zaidem, M., Ossowski, S., Martin-Pizzaro, C., Laitinen, R. A. E., Rowan, B. A., Tenenboim, H., Lechner, S., Demar, M., Habring-Muller, A., Lanz, C., Ratsch, G., et al. (2014). Species-wide genetic incompatibility analysis identifies immune genes as hot spots of deleterious epistasis. *Cell* **159**, 1341–1351.

*Chang, A. S. (2004). Conspecific sperm precedence in sister species of *Drosophila* with overlapping ranges. *Evolution* **58**, 781–789.

*Chang, A. S. & Noor, M. A. F. (2007). The genetics of hybrid male sterility between the allopatric species pair *Drosophila persimilis* and *D. pseudoobscura bogotana*: dominant sterility alleles in collinear autosomal regions. *Genetics* **176**, 343–349.

Chen, C., Zhigou, E. & Lin, H.-X. (2016). Evolution and molecular control of hybrid incompatibility in plants. *Frontiers in Plant Science* **7**, 1208.

*Chen, C. A. & Miller, D. J. (1996). Analysis of ribosoma ITS1 sequences indicates a deep divergence between *Rhodactis* (Cnidaria: Anthozoa: Corallimorpharia) species from the Caribbean and the Indo-Pacific/Red Sea. *Marine Biology* **126**, 423–432.

Chen, X., Li, S. & Aksoy, S. (1999). Concordant evolution of a symbiont with its host insect species: molecular phylogeny of genus *Glossina* and its bacteriome-associated endosymbiont, *Wigglesworthia glossinidia*. *Journal of Molecular Evolution* **48**, 49–58.

Chen, Z. & Wiens, J. J. (2020). The origins of acoustic communication in vertebrates. *Nature Communications* **11**, 369.

Chesser, R. T. & Zink, R. M. (1994). Modes of speciation in birds: a test of Lynch's method. *Evolution* **48**, 490–497.

*Civetta, A. & Gaudreau, C. (2015). Hybrid male sterility between *Drosophila willistoni* species is caused by male failure to transfer sperm during copulation. *BMC Evolutionary Biology* **15**, 75.

*Claremont, M., Reid, D. G. & Williams, S. T. (2012). Speciation and dietary specialization in *Drupa*, a genus of predatory marine snails (Gastropoda: Muricidae). *Zoologica Scripta* **41**, 137–149.

*Claridge, M. F., den Hollander, J. & Morgan, J. C. (1985). The status of weed-associated populations of the brown planthopper, *Nilaparvata lugens* (Stal): host race or biological species? *Zoological Journal of the Linnean Society* **84**, 77–90.

Clark, M. A., Moran, N. A., Baumann, P. & Wernegreen, J. J. (2000). Cospeciation between bacterial endosymbionts (*Buchnera*) and a recent radiation of aphids (*Uroleucon*) and pitfalls of testing for phylogenetic congruence. *Evolution* **54**, 517–525.

Cohan, F. M. (2001). Bacterial species and speciation. *Systematic Biology* **50**, 513–524.

Cohan, F. M. (2002). What are bacterial species? *Annual Review of Microbiology* **56**, 457e87.

Cohan, F. M. (2016). Bacterial speciation: genetic sweeps in bacterial species. *Current Biology* **26**, R112–R115.

Coleman, A. W. (2001). Biogeography and speciation in the *Pandorina/volvulina* (Chlorophyta) superclade. *Journal of Phycology* **37**, 836–851.

Coleman, A. W. (2005). *Paramecium aurelia* revisited. *Journal of Eukaryotic Microbiology* **52**, 7S–27S.

Coleman, S. W., Harlin-Cognato, A. & Jones, A. G. (2009). Reproductive isolation, reproductive mode, and sexual selection: empirical tests of the viviparity-driven conflict hypothesis. *American Naturalist* **173**, 291–303.

*Collin, R. (2003). Phylogenetic relationships among calyptraeid gastropods and their implications for the biogeography of marine speciation. *Systematic Biology* **52**, 618–640.

Colman, D. R., Toolson, E. C. & Takacs-Vesbach, C. D. (2012). Do diet and taxonomy influence insect gut bacterial communities? *Molecular Ecology* **21**, 5124–5137.

*Coluzzi, M., Sabatini, A., Della Torre, A., di Deco, M. A. & Petrarca, V. (2002). A polytene chromosome analysis of the *Anopheles gambiae* species complex. *Science* **298**, 1415–1418.

*Comeault, A. A., Serrato-capuchina, A., Turissini, D. A., Mclaughlin, P. J., David, J. R. & Matute, D. R. (2017). A nonrandom subset of olfactory genes is associated with host preference in the fruit fly *Drosophila orena*. *Evolution Letters* **1**, 73–85.

*Comesana, A. S., Toro, J. E., Innes, D. J. & Thompson, R. J. (1999). A molecular approach to the ecology of a mussel (*Mytilus edulis* - *M. trossulus*) hybrid zone on the east coast of Newfoundland, Canada. *Marine Biology* **133**, 213–221.

Connor, N., Sikorski, J., Rooney, A. P., Kopac, S., Koeppel, A. F., Burger, A., Cole, S. G., Perry, E. B., Krizanc, D., Field, N. C., Slaton, M. & Cohan, F. M. (2010). Ecology of speciation in the genus *Bacillus*. *Applied and Environmental Microbiology* **76**, 1349–1358.

Cooney, C. R., Seddon, N. & Tobias, J. A. (2016). Widespread correlations between climatic niche evolution and species diversification in birds. *Journal of Animal Ecology* **85**, 869–878.

*Coppard, S. E., Zigler, S. K. & Lessios, H. A. (2013). Phylogeography of the sand dollar genus *Mellita*: cryptic speciation along the coasts of the Americas. *Molecular Phylogenetics and Evolution* **69**, 1033–1042.

*Costantini, C., Ayala, D., Guelbeogo, W. G., Pombi, M., Some, C. Y., Bassole, I. H. N., Ose, K., Fotsing, J.-M., Sagnon, N., Fontanille, D., Besansky, N. J. & Simard, F. (2009). Living at the edge: biogeographic patterns of habitat segregation conform to speciation by niche expansion in *Anopheles gambiae*. *BMC Ecology* **9**, 16.

*Cowie, R. H. (1995). Variation in species diversity and shell shape in Hawaiian land snails: *in situ* speciation and ecological relationships. *Evolution* **49**, 1191–1202.

Coyne, J. A. & Orr, H. A. (1989). Patterns of speciation in *Drosophila*. *Evolution* **43**, 362–381.

Coyne, J. A. & Orr, H. A. (1997). "Patterns of speciation in *Drosophila*" revisited. *Evolution* **51**, 295–303.

Coyne, J. A. & Orr, H. A. (2004). *Speciation*. Sinauer, Sunderland.

*Craig, T. P., Horner, J. D. & Itami, J. K. (1997). Hybridization studies on the host races of *Eurosta solidaginis*: implications for sympatric speciation. *Evolution* **51**, 1552–1560.

*Craig, T. P., Horner, J. D. & Itami, J. K. (2001). Genetics, experience, and host-plant preference in *Eurosta solidaginis*: implications for host shifts and speciation. *Evolution* **55**, 773–782.

*Craig, T. P., Itami, J. K., Abrahamson, W. G. & Horner, J. D. (1993). Behavioral evidence for host-race formation in *Eurosta solidaginis*. *Evolution* **47**, 1696–1710.

*Craig, T. P., Itami, J. K., Shantz, C., Abrahamson, W. G., Horner, J. D. & Craig, J. V. (2000). The influence of host plant variation and intraspecific

competition on oviposition preference and offspring performance in the host races of *Eurosta solidaginis*. *Ecological Entomology* **25**, 7–18.

*CRAWFORD, J. E. & LAZZARO, B. P. (2010). The demographic histories of the M and S molecular forms of *Anopheles gambiae s.s*. *Molecular Biology and Evolution* **27**, 1739–1744.

*CRAZE, P. G. & LACE, L. A. (2000). Spatial ecology, habitat and speciation in the Porto Santan land snail genus *Heterostoma*. *Biological Journal of the Linnean Society* **71**, 665–676.

CROW, K. D., MUNEHARA, H. & BERNARDI, G. (2010). Sympatric speciation in a genus of marine reef fishes. *Molecular Ecology* **19**, 2089–2105.

*CRUAUD, A., RONSTED, N., CHANTARASUWAN, B., CHOU, L. S., CLEMENT, W. L., COULOUX, A., COUSINS, B., GENSON, G., HARRISON, R. D., HANSON, P. E., HOSSAERT-MCKEY, M., JABBOUR-ZAHAB, R., JOUSSELIN, E., KERDELHUE, C., KJELLBERG, F., et al. (2012). An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. *Systematic Biology* **61**, 1029–1047.

*CRUZ-BARRAZA, J. A., CARBALLO, J. L., ROCHA-OLIVARES, A., EHRLICH, H. & HOG, M. (2012). Integrative taxonomy and molecular phylogeny of genus *Aplysina* (Demospongiae: Verongida) from Mexican Pacific. *PLoS One* **7**, e42049.

*DAWSON, M. N. (2005). Incipient speciation of *Catostylus mosaicus* (Scyphozoa, Rhizostomeae, Catostylidae), comparative phylogeography and biogeography in south-East Australia. *Journal of Biogeography* **32**, 515–533.

*DAWSON, M. N. & JACOBS, D. K. (2001). Molecular evidence for cryptic species of *Aurelia aurita* (Cnidaria, Scyphozoa). *The Biological Bulletin* **200**, 92–96.

DAWSON, M. N. & MARTIN, L. E. (2001). Geographic variation and ecological adaptation in *Aurelia* (Scyphozoa, Semaeostomeae): some implications from molecular phylogenetics. *Hydrobiologia* **451**, 259–273.

*DE OLIVEIRA, C. C., MANFRIN, M. H., DE SENE, F. M., JACKSON, L. L. & ETGES, W. J. (2011). Variations on a theme: diversification of cuticular hydrocarbons in a clade of cactophilic *Drosophila*. *BMC Evolutionary Biology* **11**, 179.

*DE PAULA, T. S., ZILBERBERG, C., HAJDU, E. & LÔBO-HAJDU, G. (2012). Morphology and molecules on opposite sides of the diversity gradient: four cryptic species of the *Clionaelata* (Porifera, Demospongiae) complex in South America revealed by mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution* **62**, 529–541.

DE QUEIROZ, K. (2007). Species concepts and species delimitation. *Systematic Biology* **56**, 879–886.

*DELICADO, D., MACHORDOM, A. & RAMOS, M. A. (2015). Effects of habitat transition on the evolutionary patterns of the microgastropod genus *Pseudamnicola* (Mollusca, Hydrobiidae). *Zoologica Scripta* **44**, 403–417.

*DELLA TORRE, A., COSTANTINI, C., BESANSKY, N. J., CACCONE, A., PETRARCA, V., POWELL, J. R. & COLUZZI, M. (2002). Speciation within *Anopheles gambiae*: the glass is half full. *Science* **298**, 115–117.

*DEPA, L., MRÓZ, J., BUGA-NAWROCKA, A. & ORCZEWSKA, A. (2016). Do ants drive speciation in aphids? A possible case of ant-driven speciation in the aphid genus *Stomaphis* Walker (Aphidoidea, Lachninae). *Zoological Journal of the Linnean Society*. https://doi.org/10.1111/zoj.12437.

*DÉPRAZ, A., HAUSSER, J. & PFENNINGER, M. (2009). A species delimitation approach in the *Trochulus sericeus/hispidus* complex reveals two cryptic species within a sharp contact zone. *BMC Evolutionary Biology* **9**, 171.

*DESJARDINS, C. A., PERFECTTI, F., BARTOS, J. D., ENDERS, L. S. & WERREN, J. H. (2010). The genetic basis of interspecies host preference differences in the model parasitoid *Nasonia*. *Heredity* **104**, 270–277.

DETTMAN, J. R., ANDERSON, J. B. & KOHN, L. M. (2008). Divergent adaptation promotes reproductive isolation among experimental populations of the filamentous fungus *Neurospora*. *BMC Evolutionary Biology* **14**, 1–14.

*DETTMAN, J. R., JACOBSON, D. J., TURNER, E., PRINGLE, A. & TAYLOR, J. W. (2003). Reproductive isolation and phylogenetic divergence in *Neurospora*: comparing methods of species recognition in a model eukaryote. *Evolution* **57**, 2721–2741.

DETTMAN, J. R., SIRJUSINGH, C., KOHN, L. M. & ANDERSON, J. B. (2007). Incipient speciation by divergent adaptation and antagonistic epistasis in yeast. *Nature* **447**, 585–588.

DIAS, G. M., ABREU, A. G., SILVA, F. O. M. & SOLFERINI, V. N. (2009). Microgeographical differentiation between morphotypes of *Trididemnum orbiculatum* (Tunicata: Ascidiacea) in southeastern Brazil. *Aquatic Biology* **4**, 243–252.

*DIEGISSER, T., SEITZ, A. & JOHANNESEN, J. (2006). Phylogeographic patterns of host-race evolution in *Tephritis conura* (Diptera: Tephritidae). *Molecular Ecology* **15**, 681–694.

*DIXON, L. J., SCHLUB, R. L., PERNEZNY, K. & DATNOFF, L. E. (2009). Host specialization and phylogenetic diversity of *Corynespora cassiicola*. *Phytopathology* **99**, 1015–1027.

*DIXON, S. M., COYNE, J. A. & NOOR, M. A. (2003). The evolution of conspecific sperm precedence in *Drosophila*. *Molecular Ecology* **12**, 1179–1184.

*DOBZHANSKY, T. (1974). Genetic analysis of hybrid sterility within the species *Drosophila pseudoobscura*. *Hereditas* **77**, 81–88.

DONOVAN, S. E., PURDY, K. J., KANE, M. D. & EGGLETON, P. (2004). Comparison of *Euryarchaea* strains in the guts and food-soil of the soil-feeding termite *Cubitermes fungifaber* across different soil types. *Applied and Environmental Microbiology* **70**, 3884–3892.

DOOLITTLE, W. F. & PAPKE, R. T. (2006). Genomics and the bacterial species problem. *Genome Biology* **7**, 116.

*DOPMAN, E. B., BOGDANOWICZ, S. M. & HARRISON, R. G. (2004). Genetic mapping of sexual isolation between E and Z pheromone strains of the European corn borer (*Ostrinia nubilalis*). *Genetics* **167**, 301–309.

*DOPMAN, E. B., PÉREZ, L., BOGDANOWICZ, S. M. & HARRISON, R. G. (2005). Consequences of reproductive barriers for genealogical discordance in the European corn borer. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 14706–14711.

*DOPMAN, E. B., ROBBINS, P. S. & SEAMAN, A. (2010). Components of reproductive isolation between North American pheromone strains of the European corn borer. *Evolution* **64**, 881–902.

DOUHAN, G. W., SMITH, M. E., HUYRN, K. L., WESTBROOK, A., BEERLI, P. & FISHER, A. J. (2008). Multigene analysis suggests ecological speciation in the fungal pathogen *Claviceps purpurea*. *Molecular Ecology* **17**, 2276–2286.

DRÈS, M. & MALLET, J. (2002). Host races in plant-feeding insects and their importance in sympatric speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **357**, 471–492.

*DRUZHININA, I. S., KUBICEK, C. P., KOMO-ZELLAZOWSKA, M., MULAW, T. B. & BISSETT, J. (2010). The *Trichoderma harzianum* demon: complex speciation history resulting in coexistence of hypothetical biological species, recent agamospecies and numerous relict lineages. *BMC Evolutionary Biology* **10**, 94.

*DUDA, T. F. JR. & ROLAN, E. (2005). Explosive radiation of Cape Verde *Conus*, a marine species flock. *Molecular Ecology* **14**, 267–272.

*DUDA, T. F. JR. & KOHN, A. J. (2005). Species-level phylogeography and evolutionary history of the hyperdiverse marine gastropod genus *Conus*. *Molecular Phylogenetics and Evolution* **34**, 257–272.

DUVAL, L., ROBERTY, V., CSORBA, G., HASSANIN, A., RANDRIANARIVELOJOSIA, M., WALSTON, J., NHIM, T., GOODMAN, S. M. & ARIEY, F. (2007). Multiple host-switching of Haemosporidia parasites in bats. *Malaria Journal* **6**, 157.

EDWARDS, S. V., KINGAN, S. B., CALKINS, J. D., BALAKRISHNAN, C. N., JENNINGS, W. B., SWANSON, W. J. & SORENSON, M. D. (2005). Speciation in birds: genes, geography, and sexual selection. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 6550–6557.

*EGAN, S. P. & FUNK, D. J. (2009). Ecologically dependent postmating isolation between sympatric host forms of *Neochlamisus bebbianae* leaf beetles. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 19426–19431.

*EGAN, S. P., JANSON, E. M., BROWN, C. G. & FUNK, D. J. (2011). Postmating isolation and genetically variable host use in ecologically divergent host forms of *Neochlamisus bebbianae* leaf beetles. *Journal of Evolutionary Biology* **24**, 2217–2229.

*EGAN, S. P., NOSIL, P. & FUNK, D. J. (2008). Selection and genomic differentiation during ecological speciation: isolating the contributions of host association via a comparative genome scan of *Neochlamisus bebbianae* leaf beetles. *Evolution* **62**, 1162–1181.

*EITEL, M. & SCHIERWATER, B. (2010). The phylogeography of the Placozoa suggests a taxon-rich phylum in tropical and subtropical waters. *Molecular Ecology* **19**, 2315–2327.

*ELIAS, M., GOMPERT, Z., JIGGINS, C. & WILLMOTT, K. (2008). Mutualistic interactions drive ecological niche convergence in a diverse butterfly community. *PLoS Biology* **6**, e300.

*ELIAS, M., JORON, M., WILLMOTT, K., SILVA-BRANDAO, K. L., KAISER, V., ARIAS, C. F., PINEREZ, L. M. G., URIBE, S., BROWER, A. V. Z., FREITAS, A. V. L. & JIGGINS, C. D. (2009). Out of the Andes: patterns of diversification in clearwing butterflies. *Molecular Ecology* **18**, 1716–1729.

ELLSTRAND, N. C., WHITKUS, R. & RIESEBERG, L. H. (1996). Distribution of spontaneous plant hybrids. *Proceedings of the National Academy of Sciences of the United States of America* **93**, 5090–5093.

*ERPENBECK, D., KNOWLTON, A. L., TALBOT, S. L., HIGHSMITH, R. C. & VAN SOEST, R. W. M. (2004). A molecular comparison of Alaskan and Northeast Atlantic *Halichondria panicea* (Pallas 1766) (Porifera: Demospongiae) populations. *Bollettino dei Musei e degli istituti Biologici dell'Università di Genova* **68**, 319–325.

*ERPENBECK, D., WEIER, T., DE VOOGD, N. J., WÖRHEIDE, G., SUTCLIFFE, P., TODD, J. A. & MICHEL, E. (2011). Insights into the evolution of freshwater sponges (Porifera: Demospongiae: Spongillina): barcoding and phylogenetic data from Lake Tanganyika endemics indicate multiple invasions and unsettle existing taxonomy. *Molecular Phylogenetics and Evolution* **61**, 231–236.

*ESCOBAR, D., ZEA, S. & SÁNCHEZ, J. A. (2012). Phylogenetic relationships among the Caribbean members of the *Cliona viridis* complex (Porifera, Demospongiae, Hadromerida) using nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **64**, 271–284.

ESCUDERO, M. (2015). Phylogenetic congruence of parasitic smut fungi (*Anthracoidea*, Anthracoideaceae) and their host plants (*Carex*, Cyperaceae): Cospeciation or host-shift. *American Journal of Botany* **102**, 1108–1114.

EYTAN, R. I., HAYES, M., ARBOUR-REILY, P., MILLER, M. & HELLBERG, M. (2009). Nuclear sequences reveal mid-range isolation of an imperiled deep-water coral population. *Molecular Ecology* **18**, 2375–2389.

Falush, D., Torpdahl, M., Didelot, X., Conrad, D. F., Wilson, D. J. & Achtman, M. (2006). Mismatch induced speciation in *Salmonella*: model and data. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 2045–2053.

*Faucci, A., Toonen, R. J. & Hadfield, M. G. (2007). Host shift and speciation in a coral-feeding nudibranch. *Proceedings of the Royal Society B: Biological Sciences* **274**, 111–119.

*Feder, J. L., Berlocher, S. H., Roethele, J. B., Dambroski, H., Smith, J. J., Perry, W. L., Gavrilovic, V., Filchak, K. E., Rull, J. & Aluja, M. (2003a). Allopatric genetic origins for sympatric host-plant shifts and race formation in *Rhagoletis*. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 10314–10319.

*Feder, J. L. & Bush, G. L. (1989). A field test of differential host-plant usage between two sibling species of *Rhagoletis pomonella* fruit flies (Diptera: Tephritidae) and its consequences for sympatric models of speciation. *Evolution* **43**, 1813–1819.

*Feder, J. L., Roethele, J. B., Filchak, K., Niedbalski, J. & Romero-Severson, J. (2003b). Evidence for inversion polymorphism related to sympatric host race formation in the apple maggot fly, *Rhagoletis pomonella*. *Genetics* **163**, 939–953.

*Feder, J. L., Stolz, U., Lewis, K. M., Perry, W., Roethele, J. B. & Rogers, A. (1997). The effects of winter length on the genetics of apple and hawthorn races of *Rhagoletis pomonella* (Diptera: Tephritidae). *Evolution* **51**, 1862–1876.

Feliner, G. N., Alvarez, I., Fuertes-Aguilar, J., Heuertz, M., Marques, I., Moharrek, F., Pineiro, R., Riina, R., Rossello, J. A., Soltis, P. S. & Villa-Machio, I. (2017). Is homoploid hybrid speciation that rare? An empiricist's view. *Heredity* **118**, 513–516.

Fenchel, T. & Finlay, B. J. (2004). The ubiquity of small species: patterns of local and global diversity. *Bioscience* **54**, 777.

Filchak, K. E., Roethele, J. B. & Feder, J. L. (2000). Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature* **407**, 739–742.

Fitzpatrick, B. M., Fordyce, J. A. & Gavrilets, S. (2008). What, if anything, is sympatric speciation? *Journal of Evolutionary Biology* **21**, 1452–1459.

Fitzpatrick, B. M., Fordyce, J. A. & Gavrilets, S. (2009). Pattern, process and geographic modes of speciation. *Journal of Evolutionary Biology* **22**, 2342–2347.

Fitzpatrick, B. M. & Turelli, M. (2006). The geography of mammalian speciation: mixed signals from phylogenies and range maps. *Evolution* **60**, 601–615.

Forbes, A. A., Devine, S. N., Hippee, A. C., Tvedte, E. S., Ward, A. K., Widmayer, H. A. & Wilson, C. J. (2017). Revisiting the particular role of host shifts in initiating insect speciation. *Evolution* **71**, 126–137.

*Forsman, Z. H. (2003). Phylogeny and phylogeography of *Porites* and *Siderastrea* (Scleractinia: Cnidaria) species in the Caribbean and Eastern Pacific; based on the nuclear ribosomal ITS region. Doctoral Dissertation, University of Houston.

*Forsman, Z. H., Concepcion, G. T., Haverkort, R. D., Shaw, R. W., Maragos, J. E. & Toonen, R. J. (2010). Ecomorph or endangered coral? DNA and microstructure reveal Hawaiian species complexes: *Montipora dilatate/flabellate/turgescens* & *M. patula/verrilli*. *PLoS One* **5**, e15021.

*Forsman, Z. H., Guzman, H. M., Chen, C. A., Fox, G. E. & Wellington, G. M. (2005). An ITS region phylogeny of *Siderastrea* (Cnidaria: Anthozoa): is *S. glynni* endangered or introduced? *Coral Reefs* **24**, 343–347.

*Forsman, Z. H., Hunter, C. L., Fox, G. E. & Wellington, G. M. (2006). Is the ITS region the solution to the 'species problem' in corals? Intragenomic variation and alignment permutation in *Porites*, *Siderastrea*, and outgroup taxa. Proceedings of the 10th International Coral Reef Symposium, 14–23.

*Franco, F. F., Lavagnini, T. C., Sene, F. M. & Manfrin, M. H. (2015). Mito-nuclear discordance with evidence of shared ancestral polymorphism and selection in cactophilic species of *Drosophila*. *Biological Journal of the Linnean Society* **116**, 197–210.

Fraser, C., Hanage, W. P. & Spratt, B. G. (2007). Recombination and the nature of bacterial speciation. *Science* **315**, 476–480.

*Frey, M. A. (2010). The relative importance of geography and ecology in species diversification: evidence from a tropical marine intertidal snail (*Nerita*). *Journal of Biogeography* **37**, 1515–1528.

Fukami, H., Omori, M., Shimoike, K., Hayashibara, T. & Hatta, M. (2003). Ecological and genetic aspects of reproductive isolation by different spawning times in *Acropora* corals. *Marine Biology* **142**, 679–684.

*Funk, D. J. (1998). Isolating a role for natural selection in speciation: host adaptation and sexual isolation in *Neochlamisus bebbianae* leaf beetles. *Evolution* **52**, 1744–1759.

*Funk, D. J., Egan, S. P. & Nosil, P. (2011). Isolation by adaptation in *Neochlamisus* leaf beetles: host-related selection promotes neutral genomic divergence. *Molecular Ecology* **20**, 4671–4682.

*Funk, D. J., Futuyma, D. J., Orti, G. & Meyer, A. (1995). A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. *Evolution* **49**, 1008–1017.

Funk, D. J., Nosil, P. & Etges, W. J. (2006). Ecological divergence exhibits consistently positive associations with reproductive isolation across disparate taxa. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 3209–3213.

Garamszegi, L. Z. (2009). Patterns of co-speciation and host switching in primate malaria parasites. *Malaria Journal* **8**, 110.

*Garrigan, D., Kingan, S. B., Geneva, A. J., Vedanyagam, J. P. & Presgraves, D. C. (2014). Genome diversity and divergence in *Drosophila mauritiana*: multiple signatures of faster X evolution. *Genome Biology and Evolution* **6**, 2444–2458.

*Geml, J., Laursen, G. A., O'Neill, K., Nusbaum, H. C. & Taylor, D. L. (2006). Beringian origins and cryptic speciation events in the fly agaric (*Amanita muscaria*). *Molecular Ecology* **15**, 225–239.

*Gentile, G., Slotman, M., Ketmaier, V., Powell, J. R. & Caccone, A. (2001). Attempts to molecularly distinguish cryptic taxa in *Anopheles gambiae s.s. Insect Molecular Biology* **10**, 25–32.

Gevers, D., Cohan, F. M., Lawrence, J. G., Spratt, B. G., Coenye, T., Feil, E. J., Stackebrandt, E., van de Peer, Y., Vandamme, P., Thompson, F. L. & Swings, J. (2005). Re-evaluating prokaryotic species. *Nature Reviews Microbiology* **3**, 733–739.

Gibbons, J. R. H. (1979). A model for sympatric speciation in *Megarhyssa* (Hymenoptera: Ichneumonidae): competitive speciation. *American Naturalist* **114**, 719–741.

Giraud, T., Gladieux, P. & Gavrilets, S. (2010). Linking the emergence of fungal plant diseases with ecological speciation. *Trends in Ecology & Evolution* **25**, 387–395.

Giraud, T., Refrégier, G., Le Gac, M., de Vienne, D. M. & Hood, M. E. (2008). Speciation in fungi. *Fungal Genetics and Biology* **45**, 791–802.

Givnish, T. J. (2010). Ecology of plant speciation. *Taxon* **59**, 1326–1366.

*Gladieux, P., Ropars, J., Badouin, H., Branca, A., Aguileta, G., de Vienne, D. M., Rodríguez de la Vega, R. C., Branco, S. & Giraud, T. (2014). Fungal evolutionary genomics provides insight into the mechanisms of adaptive divergence in eukaryotes. *Molecular Ecology* **23**, 753–773.

Glaubrecht, M. (2011). Towards solving Darwin's "mystery": speciation and radiation in lacustrine and riverine freshwater gastropods. *American Malacological Bulletin* **29**, 187–216.

*Glazier, A. E. & Etter, R. J. (2014). Cryptic speciation along a bathymetric gradient. *Biological Journal of the Linnean Society* **113**, 897–913.

*Gleason, J. M. & Ritchie, M. G. (1998). Evolution of courtship song and reproductive isolation in the *Drosophila willistoni* species complex: do sexual signals diverge the most quickly? *Evolution* **52**, 1493–1500.

*Godefroid, M., Rocha, S., Santos, H., Paiva, M.-R., Burban, C., Kerdelhue, C., Branco, M., Rasplus, J.-Y. & Rossi, J.-P. (2016). Climate constrains range expansion of an allochronic population of the pine processionary moth. *Diversity and Distributions* **22**, 1288–1130.

*Gofas, S. (2001). The systematics of Pyrenean and Cantabrian *Cochlostoma* (Gastropoda, Cyclophoroidea) revisited. *Journal of Natural History* **35**, 1277–1369.

*Goffredi, S. K. & Barry, J. P. (2002). Species-specific variation in sulfide physiology between closely related vesicomyid clams. *Marine Ecology Progress Series* **225**, 227–238.

*Goffredi, S., Hurtado, L., Hallam, S. & Vrijenhoek, R. (2003). Evolutionary relationships of deep-sea vent and cold seep clams (Mollusca: Vesicomyidae) of the "*pacifica/lepta*" species complex. *Marine Biology* **142**, 311–320.

*Goldstien, S. J., Gemmell, N. J. & Schiel, D. R. (2006). Molecular phylogenetics and biogeography of the nacellid limpets of New Zealand (Mollusca: Patellogastropoda). *Molecular Phylogenetics and Evolution* **38**, 261–265.

*Gomes, P. B., Schama, R. & Solé-Cava, A. M. (2011). Molecular and morphological evidence that *Phymactis papillosa* from Argentina is, in fact, a new species of the genus *Bunodosoma* (Cnidaria: Actiniidae). *Journal of the Marine Biological Association of the United Kingdom* **92**, 895–910.

*Gompert, Z., Fordyce, J. A., Forister, M. L., Shapiro, A. M. & Nice, C. C. (2006). Homoploid hybrid speciation in an extreme environment. *Science* **314**, 1923–1925.

*Grace, J. L. & Shaw, K. L. (2011). Coevolution of male signal and female preference during early lineage divergence of the Hawaiian cricket, *Laupala cerasina*. *Evolution* **65**, 2184–2196.

*Grace, J. L. & Shaw, K. L. (2012). Incipient sexual isolation in *Laupala*: females discriminate acoustically differentiated populations. *Current Zoology* **58**, 416–425.

Graf, D. L. (1997). Sympatric speciation of freshwater mussels (Bivalvia: Unionoidea): a model. *American Malacological Bulletin* **14**, 35–40.

Graham, C. H., Ron, S. R., Santos, J. C., Schneider, C. J. & Moritz, C. (2004). Integrating phylogenetics and environmental niche models to explore speciation mechanisms in dendrobatid frogs. *Evolution* **58**, 1781–1793.

Grant, V. (1981). *Plant Speciation*. Columbia University Press, New York.

*Gray, D. A., Gutierrez, N. J., Chen, T. L., Gonzalez, C., Weissman, D. B. & Cole, J. A. (2016). Species divergence in field crickets: genetics, song, ecomorphology, and pre- and postzygotic isolation. *Biological Journal of the Linnean Society* **117**, 192–205.

*Grillet, M., Ferveur, J.-F. & Everaerts, C. (2018). Behavioural elements and sensory cues involved in sexual isolation between *Drosophila melanogaster* strains. *Royal Society Open Science* **5**, 172060.

GROSSENBACHER, D. L., VELOZ, S. D. & SEXTON, J. P. (2014). Niche and range size patterns suggest that speciation begins in small, ecologically diverged populations in North American monkeyflowers (*Mimulus* spp.). *Evolution* **68**, 1270–1280.

*GRUBISHA, L. C. & COTTY, P. J. (2010). Genetic isolation among sympatric vegetative compatibility groups of the aflatoxin-producing fungus *Aspergillus flavus*. *Molecular Ecology* **19**, 269–280.

*GRUNIG, C. R., MCDONALD, B. A., SIEBER, T. N., ROGERS, S. O. & HOLDENRIDER, O. (2004). Evidence for subdivision of the root-endophyte *Phialocephala fortinii* into cryptic species and recombination within species. *Fungal Genetics and Biology* **41**, 676–687.

*GUNTER, N. L. & ADLARD, R. D. (2008). Bivalvulidan (Myxozoa: Myxosporea) parasites of damselfishes with description of twelve novel species from Australia's great barrier reef. *Parasitology* **135**, 1165–1178.

*HAHN, M. W., WHITE, B. J., MUIR, C. D. & BESANSKY, N. J. (2011). No evidence for biased co–transmission of speciation islands in *Anopheles gambiae*. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367**, 374–384.

HANAGE, W. P., SPRATT, B. G., TURNER, K. M. E. & FRASER, C. (2006). Modelling bacterial speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **361**, 2039–2044.

HARDY, N. & OTTO, S. P. (2014). Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20132960.

HARRISON, P. L., BABCOCK, R. C., BULL, G. D., OLIVER, J. K., WALLACE, C. C. & WILLIS, B. L. (1984). Mass spawning in tropical reef corals. *Science* **223**, 1187–1188.

*HARRISON, R. G. (1979). Speciation in North American field crickets: evidence from electrophoretic comparisons. *Evolution* **33**, 1009–1023.

*HARRISON, R. G. (1983). Barriers to gene exchange between closely related cricket species. I. Laboratory hybridization studies. *Evolution* **37**, 245–251.

*HARRISON, R. G. (1985). Barriers to gene exchange between closely related cricket species. II. Life cycle variation and temporal isolation. *Evolution* **39**, 244–259.

*HARRISON, R. G. (1986). Pattern and process in a narrow hybrid zone. *Heredity* **56**, 337–349.

HARRISON, R. G. (2012). The language of speciation. *Evolution* **66**, 3643–3657.

*HARRISON, R. G. & BOGDANOWICZ, S. M. (1997). Patterns of variation and linkage disequilibrium in a field cricket hybrid zone. *Evolution* **51**, 493–505.

*HARRISON, R. G. & RAND, D. M. (1989). Mosaic hybrid zones and the nature of species boundaries. In *Speciation and Its Consequences* (eds D. M. OTTE and J. A. ENDLER), pp. 111–133. Sinauer Associates, Sunderland.

*HAVENS, J. A. & ETGES, W. J. (2013). Premating isolation is determined by larval rearing substrates in cactophilic *Drosophila mojavensis*. IX. Host plant and population specific epicuticular hydrocarbon expression influences mate choice and sexual selection. *Journal of Evolutionary Biology* **26**, 562–576.

*HAWTHORNE, D. J. & VIA, S. (2001). Genetic linkage of ecological specialization and reproductive isolation in pea aphids. *Nature* **412**, 904–907.

*HAYDAR, D., HOARAU, G., OLSEN, J. L., STAM, W. T. & WOLFF, W. J. (2011). Introduced or glacial relict? Phylogeography of the cryptogenetic tunicate *Molgula manhattensis* (Ascidiacea, Pleurogona). *Diversity and Distributions* **17**, 68–80.

HEGARTY, M. J. & HISCOCK, S. J. (2005). Hybrid speciation in plants: new insights from molecular studies. *New Phytologist* **165**, 411–423.

*HEITLAND, W. & PSCHORN-WALCHER, H. (1992). Biological differences between populations of *Platycampus luridiventris* feeding on different species of alder (Hymenoptera: Tenthredinidae). *Entomological Genetics* **17**, 185–194.

*HELLBERG, M. E. (1998). Sympatric sea shells along the sea's shore: the geography of speciation in the marine gastropod *Tegula*. *Evolution* **52**, 1311–1324.

*HEMBRY, D. H., KAWAKITA, A., GURR, N. E., SCHMAEDICK, M. A., BALDWIN, B. G. & GILLESPIE, R. G. (2013). Non-congruent colonizations and diversification in a coevolving pollination mutualism on oceanic islands. *Proceedings of the Royal Society B: Biological Sciences* **280**, 20130361.

*HEMERY, L. G., ELÉAUME, M., ROUSSEL, V., AMÉZIANE, N., GALLUT, C., STEINKE, D., CRUAUD, C., COULOUX, A. & WILSON, N. G. (2012). Comprehensive sampling reveals circumpolarity and sympatry in seven mitochondrial lineages of the Southern Ocean crinoid species *Promachocrinus kerguelensis* (Echinodermata). *Molecular Ecology* **21**, 2502–2518.

*HENK, D. A., EAGLE, C. E., BROWN, K., VAN DEN BERG, M. A., DYER, P. S., PETERSON, S. W. & FISHER, M. C. (2011). Speciation despite globally overlapping distributions in *Penicillium chrysogenum*: the population genetics of Alexander Fleming's lucky fungus. *Molecular Ecology* **20**, 4288–4301.

*HERBST, J. & HEITLAND, W. (1994). Genetic differentiation among populations of the sawfly species *Platycampus luridiventris*, associated with different alder species (Hymenoptera, Tenthredinidae). *Entomological Genetics* **19**, 39–48.

HERNÁNDEZ-HERNÁNDEZ, T. & WIENS, J. J. (2020). Why are there so many flowering plants? A multiscale analysis of plant diversification. *American Naturalist* **195**, 948–963.

HERRERA, C. S., HIROOKA, Y. & CHAVERRI, P. (2016). Pseudocospeciation of the mycoparasite *Cosmospora* with their fungal hosts. *Ecology and Evolution* **6**, 1504–1514.

*HERSHLER, R. & LIU, H.-P. (2008). Ancient vicariance and recent dispersal of springsnails (Hydrobiidae: *Pyrgulopsis*) in the Death Valley system, California-Nevada. *Geological Society of America Special Papers* **439**, 91–101.

*HEWITT, G. M., BUTLIN, R. K. & EAST, T. M. (2008). Testicular dysfunction in hybrids between parapatric subspecies of the grasshopper *Chorthippus parallelus*. *Biological Journal of the Linnean Society* **31**, 25–34.

*HIPPEE, A. C., ELNES, M. E., ARMENTA, J. S., CONDON, M. A. & FORBES, A. A. (2016). Divergence before the host shift? Prezygotic reproductive isolation among three varieties of a specialist fly on a single host plant. *Ecological Entomology* **4**, 389–399.

*HIROSE, E., OKA, A. T. & HIROSE, M. (2009a). Two new species of photosymbiotic ascidians of the genus *Diplosoma* from the Ryukyu archipelago, with partial sequences of the CO1 gene. *Zoological Society of Japan* **26**, 362–368.

*HIROSE, M., NOZAWA, Y. & HIROSE, E. (2010). Genetic isolation among morphotypes in the photosymbiotic didemnid *Didemnum molle* (Ascidiacea, Tunicata) from the Ryukyus and Taiwan. *Zoological Science* **27**, 959–964.

*HIROSE, M., YOKOBORI, S. & HIROSE, E. (2009b). Potential speciation of morphotypes in the photosymbiotic ascidian *Didemnum molle* in the Ryukyu archipelago, Japan. *Coral Reefs* **28**, 119–126.

*HODGE, J. R., READ, C. I., BELLWOOD, D. R. & HERWERDEN, L. (2013). Evolution of sympatric species: a case study of the coral reef fish genus *Pomacanthus* (Pomacanthidae). *Journal of Biogeography* **40**, 1676–1687.

*HOHENLOHE, P. A. (2004). Limits to gene flow in marine animals with planktonic larvae: models of *Littorina* species around Point Conception, California. *Biological Journal of the Linnean Society* **82**, 169–187.

HOLLAND, B. S. & COWIE, R. H. (2009). Land snail models in island biogeography: a tale of two snails. *American Malacological Bulletin* **27**, 59–68.

*HOLLAND, B. S. & HADFIELD, M. G. (2004). Origin and diversification of the endemic Hawaiian tree snails (Achatinellidae: Achatinellinae) based on molecular evidence. *Molecular Phylogenetics and Evolution* **32**, 588–600.

*HOLZER, A. S., BARTOŠOVÁ, P., PECKTOVÁ, H., TYML, T., ATKINSON, S., BARTHOLOMEW, J., SIPOS, D., ESZTERBAUER, E. & DYKOVÁ, I. (2012). 'Who's who' in renal sphaerosporids (Bivalvulia: Myxozoa) from common carp, Prussian carp and goldfish—molecular identification of cryptic species, blood stages and new members of *Sphaerospora sensu stricto*. *Parasitology* **140**, 46–60.

*HONEY-ESCANDÓN, M., LAGUARDA-FIGUERAS, A. & SOLÍS-MARÍN, F. A. (2012). Molecular phylogeny of the subgenus *Holothuria* (Selenkothuria) Deichmann, 1958 (Holothuroidea: Aspidochirotida). *Zoological Journal of the Linnean Society* **165**, 109–120.

*HORNDER, J. D., CRAIG, T. P. & ITAMI, J. K. (1999). The influence of oviposition phenology on survival in host races of *Eurosta solidaginis*. *Entomologia Experimentalis et Applicata* **93**, 121–129.

HOSKIN, C. J., HIGGIE, M., MCDONALD, K. R. & MORITZ, C. (2005). Reinforcement drives rapid allopatric speciation. *Nature* **437**, 1353–1356.

HOSOKAWA, T., KIKUCHI, Y., NIKOH, N., SHIMADA, M. & FUKATSU, T. (2006). Strict host-symbiont cospeciation and reductive genome evolution in insect gut bacteria. *PLoS Biology* **4**, e337.

HOSOKAWA, T., NIKOH, N., KOGA, R., SATO, M., TANAHASHI, M., MENG, X.-Y. & FUKATSU, T. (2012). Reductive genome evolution, host-symbiont co-speciation and uterine transmission of endosymbiotic bacteria in bat flies. *ISME Journal* **6**, 577–587.

HOU, J., FOURNIER, T. & SCHACHERER, J. (2016). Species-wide survey reveals the various flavors of intraspecific reproductive isolation in yeast. *FEMS Yeast Research* **16**, 1–8.

*HOWELL, K. L., ROGERS, A. D., TYLER, P. A. & BILLETT, D. S. M. (2004). Reproductive isolation among morphotypes of the Atlantic seastar species *Zoroaster fulgens* (Asteroidea: Echinodermata). *Marine Biology* **144**, 977–984.

*HRINCEVICH, A. W., ROCHA-OLIVARES, A. & FOLTZ, D. W. (2000). Phylogenetic analysis of molecular lineages in a species-rich subgenus of sea stars (*Leptasterias* subgenus *Hexasterias*). *American Zoologist* **40**, 365–374.

HUA, X. & WIENS, J.J. (2010). Latitudinal variation in speciation mechanisms in frogs. *Evolution* **64**, 429–443.

HUA, X. & WIENS, J. J. (2013). How does climate influence speciation? *American Naturalist* **182**, 1–12.

HUGHES, A. L. & VERRA, F. (2010). Malaria parasite sequences from chimpanzee support the co-speciation hypothesis for the origin of virulent human malaria (*Plasmodium falciparum*). *Molecular Phylogenetics and Evolution* **57**, 135–143.

*HUNTER, R. L. & HALANYCH, K. A. (2008). Evaluating connectivity in the brooding brittle star *Astrotoma agassizii* across the Drake Passage in the Southern Ocean. *Journal of Heredity* **99**, 137–148.

IMADA, Y., KAWAKITA, A. & KATO, M. (2011). Allopatric distribution and diversification without niche shift in a bryophyte-feeding basal moth lineage (Lepidoptera: Micropterigidae). *Proceedings of the Royal Society B: Biological Sciences* **278**, 3026–3033.

INGRAM, T. (2011). Speciation along a depth gradient in a marine adaptive radiation. *Proceedings of the Royal Society B: Biological Sciences* **278**, 613–618.

*Inoue, K., McQueen, A. L., Harris, J. L. & Berg, D. J. (2014). Molecular phylogenetics and morphological variation reveal recent speciation in freshwater mussels of the genera *Arcidens* and *Arkansia* (Bivalvia: Unionidae). *Biological Journal of the Linnean Society* **112**, 535–545.

*Itami, J., Craig, T. & Horner, J. (1998). Factors affecting gene flow between the host races of *Eurosta solidaginis*. In *Genetic Structure and Local Adaptation in Natural Insect Populations: Effects of Ecology, Life History, and Behavior* (eds S. Mopper and S. Strauss), pp. 375–404. Chapman & Hall, New York.

Jackson, A. P. (2004). A reconciliation analysis of host switching in plant-fungal symbioses. *Evolution* **58**, 1909–1923.

Jančúchová-Lásková, J., Landová, E. & Frynta, D. (2015). Are genetically distinct lizard species able to hybridize? A review. *Current Zoology* **61**, 155–180.

Janz, N. (2011). Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution, and Systematics* **42**, 71–89.

*Jargeat, P., Martos, F., Carriconde, F., Gryta, H., Moreau, P. A. & Gardes, M. (2010). Phylogenetic species delimitation in ectomycorrhizal fungi and implications for barcoding: the case of the *Tricholoma scalpturatum* complex (Basidiomycota). *Molecular Ecology* **19**, 5216–5230.

Jezkova, T. & Wiens, J. J. (2018). Testing the role of climate in speciation: new methods and applications to squamate reptiles (lizards and snakes). *Molecular Ecology* **27**, 2754–2769.

Jiggins, C. D. (2008). Ecological speciation in mimetic butterflies. *Bioscience* **58**, 541–548.

*Jiggins, C. D. (2016). The Ecology and Evolution of Heliconius Butterflies. Oxford University Press, Oxford.

Jiggins, C. D., Mallarino, R., Willmott, K. R., Bermingham, E. & Funk, D. (2006). The phylogenetic pattern of speciation and wing pattern change in neotropical *Ithomia* butterflies (Lepidoptera: Nymphalidae). *Evolution* **60**, 1454–1466.

*Jiggins, C. D., Salazar, C. & Mavarez, J. (2008). Hybrid trait speciation and *Heliconius* butterflies. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 3047–3054.

Jordaens, K., van Riel, P., Frias Martins, A. M. & Backeljau, T. (2009). Speciation on the Azores islands: congruent patterns in shell morphology, genital anatomy, and molecular markers in endemic land snails (Gastropoda, Leptaxinae). *Biological Journal of the Linnean Society* **97**, 166–176.

*Jordal, B. H. (2006). Community structure and reproductive biology of bark beetles (Coleoptera: Scolytinae) associated with Macaronesian *Euphorbia* shrubs. *European Journal of Entomology* **103**, 71–80.

*Jordal, B. H., Emerson, B. C. & Hewitt, G. M. (2006). Apparent 'sympatric' speciation in ecologically similar herbivorous beetles facilitated by multiple colonizations of an island. *Molecular Ecology* **15**, 2935–2947.

*Jordal, B. H., Hewitt, G. M. & Whitfield, J. (2004). The origin and radiation of Macaronesian beetles breeding in *Euphorbia*: the relative importance of multiple data partitions and population sampling. *Systematic Biology* **53**, 711–734.

*Jousselin, E., Cruaud, A., Genson, G., Chevenet, F., Foottit, R. G. & Couer d'Acier, A. (2013). Is ecological speciation a major trend in aphids? Insights from a molecular phylogeny of the conifer-feeding genus *Cinara*. *Frontiers in Zoology* **10**, 56.

*Kambysellis, M. P. & Craddock, E. M. (1997). Ecological and reproductive shifts in the diversification of the endemic Hawaiian *Drosophila*. In *Molecular Evolution and Adaptive Radiation* (eds T. J. Gvinish and K. J. Sytsma), pp. 475–509. Cambridge University Press, Cambridge, UK.

Kamimura, Y. & Mitsumoto, H. (2012). Lock-and-key structural isolation between sibling *Drosophila* species. *Entomological Science* **15**, 197–201.

Kamiya, M., West, J. A., King, R. J., Zuccarello, G. C., Tanaka, J. & Hara, Y. (1998). Evolutionary divergence in the red algae *Caloglossa leprieurii* and *C. apomeiotica*. *Journal of Phycology* **34**, 361–370.

*Kang, J.-C., Crous, P. W. & Schoch, C. L. (2001). Species concepts in the *Cylindrocladium floridanum* and *Cy. spathiphylli* complexes (Hypocreaceae) based on multi-allelic sequence data, sexual compatibility and morphology. *Systematic and Applied Microbiology* **24**, 206–217.

*Katakura, H. (1997). Species of *Epilachna* ladybird beetles. *Zoological Science* **14**, 869–881.

*Katakura, H. & Hosogai, T. (1997). Host preference of F1 hybrids between two host specific phytophagous ladybird beetles (*Epilachna* spp., Epilachninae, Coccinellidae). *Japanese Journal of Entomology* **65**, 75–79.

*Katakura, H. & Nakano, S. (1979). Preliminary experiments on the crossing between two puzzling phytophagous ladybirds, *Henosepilachna vigintioctomaculata* and *H. pustulosa* (Coleoptera: Coccinellidae). *Kontyû (Tokyo)* **47**, 176–184.

*Katakura, H., Saitoh, S. & Aoki, M. (1996). Sexual isolation between three forms of flightless *Chrysolina* beetles (Coleoptera: Chrysomelidae) parapatrically distributed in the vicinity of Sapporo, Hokkaido, northern Japan. *Genes and Genetic Systems* **71**, 139–144.

*Katakura, H., Shioi, M. & Kira, Y. (1989). Reproductive isolation by host specificity in a pair of phytophagous ladybird beetles. *Evolution* **43**, 1045–1053.

*Kauserud, H., Stensrud, Ø., Decock, C., Shalchian-Tabrizi, K. & Schumacher, T. (2006). Multiple gene genealogies and AFLPs suggest cryptic speciation and long-distance dispersal in the basidiomycete *Serpula himantioides* (Boletales). *Molecular Ecology* **15**, 421–431.

Kay, K. M. & Sargent, R. D. (2009). The role of animal pollination in plant speciation: integrating ecology, geography, and genetics. *Annual Review Ecology, Evolution, and Systematics* **40**, 637–656.

Kergoat, G. J., Meseguer, A. S. & Jousselin, E. (2017). Evolution of plant-insect interactions: insights from macroevolutionary approaches in plants and herbivorous insects. In *Insect-Plant Interactions in a Crop Protection Perspective* (Volume **81**, eds D. T. N. Sauvion and P.-A. Calatayud), pp. 25–53. Academic Press, Cambridge.

*Keese, M. C. (1996). Feeding responses of hybrids and the inheritance of host-use traits in leaf feeding beetles (Coleoptera: Chrysomelidae). *Heredity* **76**, 36–42.

*Kelly, R. P. & Eernisse, D. J. (2008). Reconstructing a radiation: the chiton genus *Mopalia* in the North Pacific. *Invertebrate Systematics* **22**, 17–28.

Kikuchi, Y., Hosokawa, T., Nikoh, N., Meng, X.-Y., Kamagata, Y. & Fukatsu, T. (2009). Host-symbiont co-speciation and reductive genome evolution in gut symbiotic bacteria of acanthosomatid stinkbugs. *BMC Biology* **7**, 2.

Kikuchi, Y., Meng, X.-Y. & Fukatsu, T. (2005). Gut symbiotic bacteria of the genus *Burkholderia* in the broad-headed bugs *Riptortus clavatus* and *Leptocorisa chinensis* (Heteroptera: Alydidae). *Applied and Environmental Microbiology* **71**, 4035–4043.

*Kim, S. W., Kerr, A. M. & Paulay, G. (2013). Colour, confusion, and crossing: resolution of species problems in *Bohadschia* (Echinodermata: Holothuroidea). *Zoological Journal of the Linnean Society* **168**, 81–97.

*Kim, Y.-K., Phillips, D. R., Chao, T. & Eerhman, L. (2004). Developmental isolation and subsequent adult behavior of *Drosophila paulistorum*. VI. Quantitative variation in cuticular hydrocarbons. *Behavior Genetics* **34**, 385–394.

*Kim, Y.-K., Ruiz-Garcia, M., Alvarez, D., Phillips, D. R. & Anderson, W. W. (2012). Sexual isolation between North American and Bogota strains of *Drosophila pseudoobscura*. *Behavior Genetics* **42**, 472–482.

*Kiss, L., Pintye, A., Kovac, G. M., Jankovics, T., Fontaine, M. C., Harvey, N., Xu, X., Nicot, P. C., Bardin, M., Shykoff, J. A. & Giraud, T. (2011). Temporal isolation explains host-related genetic differentiation in a group of widespread mycoparasitic fungi. *Molecular Ecology* **20**, 1492–1507.

*Klautau, M., Russo, C. A., Lazoski, C., Boury-Esnault, N., Thorpe, J. P. & Solé-Cava, A. M. (1999). Does cosmopolitanism result from overconservative systematics? A case study using the marine sponge *Chondrilla nucula*. *Evolution* **53**, 1414–1422.

Knowlton, N. (1993). Sibling species in the sea. *Annual Review of Ecology and Systematics* **24**, 189–216.

*Knowlton, N. (2000). Molecular genetic analysis of species boundaries in the sea. *Hydrobiologia* **420**, 73–90.

*Kohler, F. & Glaubrecht, M. (2010). Uncovering an overlooked radiation: molecular phylogeny and biogeography of Madagascar's endemic river snails (Caenogastropoda: Pachychilidae: *Madagasikara* gen. nov.). *Biological Journal of the Linnean Society* **99**, 867–894.

Kohn, L. M. (2005). Mechanisms of fungal speciation. *Annual Review of Phytopathology* **43**, 279–308.

*Komazaki, S. (1986). The inheritance of egg hatch timing of the overwintering egg among populations of *Aphis citricola* Van der Groot (Homoptera: Aphididae) on the two winter hosts. *Kontyu* **54**, 48–53.

*Komazaki, S. (1990). Variation in the hatch timing of the overwintering egg among populations of *Aphis spiraecola* patch (Homoptera: Aphididae) collected from different host plants and localities in Japan. *Applied Entomology and Zoology* **25**, 27–34.

*Komazaki, S. (1998). Difference of egg diapause in two host races of the spiraea aphid, *Aphis spiraecola*. *Entomologia Experimentalis et Applicata* **89**, 201–205.

*Kon, T., Nohara, M., Nishida, M., Sterrer, W. & Nishikawa, T. (2006). Hidden ancient diversification in the circumtropical lancelet *Asymmetron lucayanum* complex. *Marine Biology* **149**, 875–883.

*Kongjandtre, N., Ridgway, T., Cook, L. G., Huelsken, T., Budd, A. F. & Hoegh-Guldberg, O. (2012). Taxonomy and species boundaries in the coral genus *Favia* Milne Edwards and Haime, 1857 (Cnidaria: Scleractinia) from Thailand revealed by morphological and genetic data. *Coral Reefs* **31**, 581–601.

*Korábek, O., Petrusek, A., Neubert, E. & Juricková, L. (2015). Molecular phylogeny of the genus *Helix* (Pulmonata: Helicidae). *Zoologica Scripta* **44**, 263–280.

*Koref-Santibánez, S. (2001). Effects of age and experience on mating activity in the sibling species *Drosophila pavani* and *Drosophila gaucha*. *Behavior Genetics* **31**, 287–297.

*Koufopanou, V., Burt, A. & Taylor, J. W. (1997). Concordance of gene genealogies reveals reproductive isolation in the pathogenic fungus *Coccidioides immitis*. *Proceedings of the National Academy of Sciences of the United States of America* **94**, 5478–5482.

Kozak, K. H. & Wiens, J. J. (2006). Does niche conservatism promote speciation? A case study in North American salamanders. *Evolution* **60**, 2604–2621.

Kozak, K. H. & Wiens, J. J. (2010). Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters* **13**, 1378–1389.

Kozak, K. H. & Wiens, J. J. (2016). Testing the relationships between diversification, species richness, and trait evolution. *Systematic Biology* **65**, 975–988.

*Kreslavsky, A. G. & Mikheyev, A. V. (1993). Gene geography and racial differences in *Lochmaea capreae* L. (Coleoptera, Chrysomelidae), and the problem of sympatric speciation. *Zoologichesky Zhurnal* **72**, 50–58.

*Kronforst, M. R., Young, L. G., Kapan, D. D., McNeely, C., O'Neill, R. J. & Gilbert, L. E. (2006). Linkage of butterfly mate preference and wing color preference cue at the genomic location of wingless. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6575–6580.

Krug, P. J. (2011). Patterns of speciation in marine gastropods: a review of the phylogenetic evidence for localized radiations in the sea. *American Malacological Bulletin* **29**, 169–186.

*Kuehne, H. A., Murphy, H. A., Francis, C. A. & Sniegowski, P. D. (2007). Allopatric divergence, secondary contact, and genetic isolation in wild yeast populations. *Current Biology* **17**, 407–411.

Lajeunesse, T. C. & Thornhill, D. J. (2011). Improved resolution of reef-coral endosymbiont (*Symbiodinium*) species diversity, ecology, and evolution through psbA non-coding region genotyping. *PLoS One* **6**, e29013.

Landry, C., Geyer, L. B., Arakaki, Y., Uehara, T. & Palumbi, S. R. (2003). Recent speciation in the Indo-West Pacific: rapid evolution of gamete recognition and sperm morphology in cryptic species of sea urchin. *Proceedings of the Royal Society B: Biological Sciences* **270**, 1839–1847.

Larsen, B. B., Miller, E. C., Rhodes, M. K. & Wiens, J. J. (2017). Inordinate fondness multiplied and redistributed: the number of species on earth and the new Pie of Life. *Quarterly Review of Biology* **92**, 229–265.

*Larson, E. L., Andrés, J. A. & Harrison, R. G. (2012). Influence of the male ejaculate on post-mating prezygotic barriers in field crickets. *PLoS One* **7**, e46202.

Lassalle, F., Muller, D. & Nesme, X. (2015). Ecological speciation in bacteria: reverse ecology approaches reveal the adaptive part of bacterial cladogenesis. *Research in Microbiology* **166**, 729–741.

*Lassance, J. M., Groot, A. T., Liénard, M. A., Antony, B., Borgwardt, C., Andersson, F., Hedenstrom, E., Heckel, D. G. & Lofstedt, C. (2010). Allelic variation in a fatty-acyl reductase gene causes divergence in moth sex pheromones. *Nature* **466**, 486–489.

*Lawniczak, M. K. N., Emrich, S. J., Holloway, A. K., Regier, A. P., Olson, M., White, B., Redmond, S., Fulton, L., Applebaum, E., Godfrey, J., Farmer, C., Chinwalla, A., Yang, S.-P., Minx, P., Nelson, J., et al. (2010). Widespread divergence between incipient *Anopheles gambiae* species revealed by whole-genome sequences. *Science* **330**, 512–514.

Lawrence, J. G. & Retchless, A. C. (2010). The myth of bacterial species and speciation. *Biology and Philosophy* **25**, 569–588.

Lazarus, D. (1983). Speciation in pelagic Protista and its study in the planktonic microfossil record: a review. *Paleobiology* **9**, 327–340.

*Lazoski, C., Solé-Cava, A., Boury-Esnault, N., Klautau, M. & Russo, C. (2001). Cryptic speciation in a high gene flow scenario in the oviparous marine sponge *Chondrosia reniformis*. *Marine Biology* **139**, 421–429.

Le Gac, M. & Giraud, T. (2008). Existence of a pattern of reproductive character displacement in Homobasidiomycota but not in Ascomycota. *Journal of Evolutionary Biology* **21**, 761–772.

*Leavitt, S. D., Fankhauser, J. D., Leavitt, D. H., Porter, L. D., Jonhson, L. A. & St. Clair, L. L. (2011). Complex patterns of speciation in cosmopolitan 'rock posy' lichens - discovering and delimiting cryptic fungal species in the lichen-forming *Rhizoplaca melanophthalma* species-complex (Lecanoraceae, Ascomycota). *Molecular Phylogenetics and Evolution* **59**, 587–602.

*Lee, T. & Foighil, D. (2005). Placing the Floridian marine genetic disjunction into a regional evolutionary context using the scorched mussel, *Brachidontes exustus*, species complex. *Evolution* **59**, 2139–2158.

Lefevre, C., Charles, H., Vallier, A., Delobel, B., Farrell, B. & Heddi, A. (2004). Endosymbiont phylogenesis in the Dryophthoridae weevils: evidence for bacterial replacement. *Molecular Biology and Evolution* **21**, 965–973.

Lessios, H. A. (2007). Reproductive isolation between species of sea urchins. *Bulletin of Marine Science* **81**, 191–208.

Lessios, H. A. (2011). Speciation genes in free-spawning marine invertebrates. *Integrative and Comparative Biology* **51**, 456–465.

*Li, J., Doighil, D. Ó. & Park, J.-K. (2013). Triton's trident: cryptic Neogene divergences in a marine clam (*Lasaea australis*) correspond to Australia's three temperate biogeographic provinces. *Molecular Ecology* **22**, 1933–1946.

Linnen, C. R. & Farrell, B. D. (2010). A test of the sympatric host race formation hypothesis in *Neodiprion* (Hymenoptera: Diprionidae). *Proceedings of the Royal Society of London B: Biological Sciences* **277**, 3131–3138.

*Linnen, C. R. & Smith, D. R. (2012). Recognition of two additional pine-feeding *Neodiprion* species (Hymenoptera: Diprionidae) in the eastern United States. *Proceedings of the Entomological Society of the Washington* **114**, 492–500.

*Linz, J., Baschwitz, A., Strutz, A., Dweck, H. K. M., Sachse, S., Hansson, B. S. & Stensmyr, M. C. (2013). Host plant-driven sensory specialization in *Drosophila erecta*. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20130626.

Liti, G., Barton, D. B. H. & Louis, E. J. (2006). Sequence diversity, reproductive isolation and species concepts in *Saccharomyces*. *Genetics* **174**, 839–850.

Lo, N., Bandi, C., Watanabe, H., Nalepa, C. & Beninati, T. (2003). Evidence for cocladogenesis between diverse dictyopteran lineages and their intracellular endosymbionts. *Molecular Biology and Evolution* **20**, 907–913.

Loeblich, A. R., Schmidt, R. J. & Sherley, J. (1981). Scanning electron microscopy of *Heterocapsa pygmaea* sp. nov., and evidence for polyploidy as a speciation mechanism in dinoflagellates. *Journal of Plankton Research* **3**, 67–79.

Losos, J. B. & Glor, R. E. (2003). Phylogenetic comparative methods and the geography of speciation. *Trends in Ecology and Evolution* **18**, 220–227.

Louca, S., Mazel, F., Doebeli, M. & Parfrey, L. W. (2019). A census-based estimate of Earth's bacterial and archaeal diversity. *PLoS Biology* **17**, e3000106.

Lowry, D. B., Modliszewski, J. L., Wright, K. M., Wu, C. A. & Willis, J. H. (2008). The strength and genetic basis of reproductive isolating barriers in flowering plants. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 3009–3021.

*Lukhtanov, V. A. (2012). The geography of speciation in butterflies (Lepidoptera, Papilionoidea): an empirical test of theoretical models. *Entomological Review* **92**, 46–54.

*Lukhtanov, V. A., Kandul, N. P., Plotkin, J. B., Dantchenko, A. V., Haig, D. & Pierce, N. E. (2005). Reinforcement of prezygotic isolation and karyotype evolution in *Agrodiaetus* butterflies. *Nature* **436**, 385–389.

Lynch, J. D. (1989). The gauge of speciation: on the frequency of modes of speciation. In *Speciation and its Consequences* (eds D. Otte and J. A. Endler), pp. 527–553. Sinauer Associates, Sunderland.

Maan, M. E. & Seehausen, O. (2011). Ecology, sexual selection and speciation. *Ecology Letters* **14**, 591–602.

Magallón, S. & Sanderson, M. J. (2001). Absolute diversification rates in angiosperm clades. *Evolution* **55**, 1762–1780.

*Maggioni, D., Montano, S., Seveso, D. & Galli, P. (2016). Molecular evidence for cryptic species in *Pteroclava krempfi* (Hydrozoa, Cladocorynidae) living in association with alcyonaceans. *Systematics and Biodiversity* **14**, 484–493.

Maggs, C. A., Fletcher, H. L., Fewer, D., Loade, L., Mineur, F. & Johnson, M. P. (2011). Speciation in red algae: members of the Ceramiales as model organisms. *Integrative and Comparative Biology* **51**, 492–504.

*Mah, C. L. (2006). Phylogeny and biogeography of the deep-sea goniasterid *Circeaster* (Echinodermata, Asteroidea, Goniasteridae) including descriptions of six new species. *Zoosystema* **28**, 917–954.

*Mah, C., Nizinski, M. & Lundsten, L. (2010). Phylogenetic revision of the Hippasterinae (Goniasteridae; Asteroidea): systematics of deep sea corallivores, including one new genus and three new species. *Zoological Journal of the Linnean Society* **160**, 266–301.

*Malaquias, M. A. E. & Reid, D. G. (2009). Tethyan vicariance, relictualism and speciation: evidence from a global molecular phylogeny of the opisthobranch genus *Bulla*. *Journal of Biogeography* **36**, 1760–1777.

*Malausa, T., Bethenod, M.-T., Bontemps, A., Bourguet, D., Crnuet, J.-M. & Ponsard, S. (2005). Assortative mating in sympatric host- races of the European corn borer. *Science* **308**, 258–260.

*Mallet, J. (2008). Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**, 2971–2986.

Malone, J. H. & Fontenot, B. E. (2008). Patterns of reproductive isolation in toads. *PLoS One* **3**, e3900.

*Manoukis, N. C., Powell, J. R., Touré, M. B., Sacko, A., Edillo, F. E., Coulibaly, M. B., Traoré, S. F., Taylor, C. E. & Besansky, N. J. (2008). A test of the chromosomal theory of ecotypic speciation in *Anopheles gambiae*. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 2940–2945.

*Marko, P. B. (2002). Fossil calibration of molecular clocks and the divergence times of geminate species pairs separated by the isthmus of Panama. *Molecular Biology and Evolution* **19**, 2005–2021.

*Marko, P. B. & Moran, A. L. (2009). Out of sight, out of mind: high cryptic diversity obscures the identities and histories of geminate species in the marine bivalve subgenus *Acar*. *Journal of Biogeography* **36**, 1861–1880.

*Maroja, L. S., Andrés, J. A. & Harrison, R. G. (2009a). Genealogical discordance and patterns of introgression and selection across a cricket hybrid zone. *Evolution* **63**, 2999–3015.

*Maroja, L. S., Andrés, J. A., Walters, J. R. & Harrison, R. G. (2009b). Multiple barriers to gene exchange in a field cricket hybrid zone. *Biological Journal of the Linnean Society* **97**, 390–402.

*Marshall, D. C., Slon, K., Cooley, J. R., Hill, K. B. & Simon, C. (2008). Steady Plio-Pleistocene diversification and a 2-million-year sympatry threshold

in a New Zealand cicada radiation. *Molecular Phylogenetics and Evolution* **48**, 1054–1066.

MARTIN, M. D. & MENDELSON, T. C. (2015). The accumulation of reproductive isolation in early stages of divergence supports a role for sexual selection. *Journal of Evolutionary Biology* **29**, 676–689.

MARTIN, M. D. & MENDELSON, T. C. (2018). Hybrid sterility increases with genetic distance in snubnose darters (Percidae: *Etheostoma*). *Environmental Biology of Fishes* **101**, 215–221.

*MARTÍNEZ, D. E., IÑIGUEZ, A. R., PERCELL, K. M., WILLNER, J. B., SIGNOROVITCH, J. & CAMPBELL, R. D. (2010). Phylogeny and biogeography of *Hydra* (Cnidaria: Hydridae) using mitochondrial and nuclear DNA sequences. *Molecular Phylogenetics and Evolution* **57**, 403–410.

MASON, N. A., BURNS, K. J., TOBIAS, J. A., CLARAMUNT, S., SEDDON, N. & DERRYBERRY, E. P. (2017). Song evolution, speciation, and vocal learning in passerine birds. *Evolution* **71**, 786–796.

*MATÉ, J. L. (2003). Ecological, genetic, and morphological differences among three *Pavona* (Cnidaria: Anthozoa) species from the Pacific coast of Panama. *Marine Biology* **142**, 427–440.

*MATSUBAYASHI, K. W. & KATAKURA, H. (2007). Unilateral mate choice causes bilateral behavioral isolation between two closely related phytophagous ladybird beetles (Coleoptera: Coccinellidae: Epilachninae). *Ethology* **113**, 686–691.

*MATSUBAYASHI, K. W. & KATAKURA, H. (2009). Contribution of multiple isolating barriers to reproductive isolation between a pair of phytophagous ladybird beetles. *Evolution* **63**, 2563–2580.

MATSUBAYASHI, K. W., OHSHIMA, I. & NOSIL, P. (2010). Ecological speciation in phytophagous insects. *Entomologia Experimentalis et Applicata* **134**, 1–27.

*MATSUDA, M., TOMIMURA, Y. & TOBARI, Y. N. (2005). Reproductive isolation among geographical populations of *Drosophila bipectinata* Duda (Diptera, Drosophilidae) with recognition of three subspecies. *Genetica* **125**, 69–78.

*MATUTE, D. R., McEWEN, J. G., PUCCIA, R., MONTES, B. A., SAN-BLAS, G., BAGAGLI, E., RAUSCHER, J. T., RESTREPO, A., MORAIS, F., NINO-VEGA, G. & TAYLOR, J. W. (2006). Cryptic speciation and recombination in the fungus *Paracoccidioides brasiliensis* as revealed by gene genealogies. *Molecular Biology and Evolution* **23**, 65–73.

*MATUTE, D. R., NOVAK, C. J. & COYNE, J. A. (2009). Temperature-based extrinsic reproductive isolation in two species of *Drosophila*. *Evolution* **63**, 595–612.

*MATZKIN, L. M. (2014). Ecological genomics of host shifts in *Drosophila mojavensis*. In *Ecological Genomics. Advances in Experimental Medicine and Biology* (Volume **781**, eds C. LANDRY and N. AUBIN-HORTH). Springer, Dordrecht.

*MAVÁREZ, J., SALAZAR, C. A., BERMINGHAM, E., SALCEDO, C., JIGGINS, C. D. & LINARES, M. (2006). Speciation by hybridization in *Heliconius* butterflies. *Nature* **441**, 868–871.

*McALLISTER, B. F., SHEELEY, S. L., MENA, P. A., EVANS, A. L. & SCHLOTTERER, C. (2008). Clinal distribution of a chromosomal rearrangement: a precursor to chromosomal speciation? *Evolution* **62**, 1852–1865.

*McBRIDE, C. S., VAN VELZEN, R. & LARSEN, T. B. (2009). Allopatric origin of cryptic butterfly species that were discovered feeding on distinct host plants in sympatry. *Molecular Ecology* **18**, 3639–3651.

McCLARY, D. J. & SEWELL, M. A. (2002). Hybridization in the sea: gametic and developmental constraints on fertilization in sympatric species of *Pseudechinus* (Echinodermata: Echinoidea). *Journal of Experimental Marine Biology and Ecology* **284**, 51–70.

McFADDEN, C. S. & HUTCHINSON, M. B. (2004). Molecular evidence for the hybrid origin of species in the soft coral genus *Alcyonium* (Cnidaria: Anthozoa: Octocorallia). *Molecular Ecology* **13**, 1495–1505.

*MENDELSON, T. C. & SHAW, K. L. (2005). Sexual behaviour: rapid speciation in an arthropod. *Nature* **433**, 375–376.

MERCKX, V. & BIDARTONDO, M. I. (2008). Breakdown and delayed cospeciation in the arbuscular mycorrhizal mutualism. *Proceedings of the Royal Society B: Biological Sciences* **275**, 1029–1035.

*MÉROT, C., SALAZAR, C., MERRILL, R. M. & JIGGINS, C. D. (2017). What shapes the continuum of reproductive isolation? Lessons from *Heliconius* butterflies. *Proceedings of the Royal Society B: Biological Sciences* **284**, 2017033.

*MEROZ-FINE, E., BRICKNER, I., LOYA, Y. & ILAN, M. (2003). The hydrozoan coral *Millepora dichotoma*: speciation or phenotypic plasticity? *Marine Biology* **143**, 1175–1183.

*MESEGUER, A. S., COEUR D'ACIER, A., GENSON, G. & JOUSSELIN, E. (2015). Unravelling the historical biogeography and diversification dynamics of a highly diverse conifer-feeding aphid genus. *Journal of Biogeography* **42**, 1482–1492.

MEYER, A. L. S., ROMÁN-PALACIOS, C. & WIENS, J. J. (2018). BAMM gives misleading rate estimates in simulated and empirical datasets. *Evolution* **72**, 2257–2266.

*MEYER, C. P. (2003). Molecular systematics of cowries (Gastropoda: Cypraeidae) and diversification patterns in the tropics. *Biological Journal of the Linnean Society* **79**, 401–459.

*MICHEL, E. (2000). Phylogeny of a gastropod species flock: exploring speciation in Lake Tanganyika in a molecular framework. *Advances in Ecological Research* **31**, 275–302.

*MICHONNEAU, F., McPHERSON, S., O'LOUGHLIN, P. M. & PAULAY, G. (2015). More than meets the eye: diversity and geographic patterns in sea cucumbers. *bioRxiv*014282.

*MIGLIETTA, M. P., PIRAINO, S., KUBOTA, S. & SCHUCHER, P. (2006). Species in the genus *Turritopsis* (Cnidaria, Hydrozoa): a molecular evaluation. *Journal of Zoological Systematics and Evolutionary Research* **45**, 11–19.

*MIKKELSEN, P. M. (2011). Speciation in modern marine bivalves (Mollusca: Bivalvia): insights from the published record. *American Malacological Bulletin* **29**, 217–245.

*MILLER, K., ALVAREZ, B., BATTERSHILL, C., NORTHCOTE, P. & PARTHASARATHY, H. (2001). Genetic, morphological, and chemical divergence in the sponge genus *Latrunculia* (Porifera: Demospongiae) from New Zealand. *Marine Biology* **139**, 235–250.

MITTER, C., FARRELL, B. & WIEGMANN, B. (1988). The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? *American Naturalist* **132**, 107–128.

*MOEHRING, A. J., LLOPART, A., ELWYN, S., COYNE, J. A. & MACKAY, T. F. C. (2006). The genetic basis of postzygotic reproductive isolation between *Drosophila santomea* and *D. yakuba* due to hybrid male sterility. *Genetics* **173**, 225–233.

MOEN, D. S. & WIENS, J. J. (2017). Microhabitat and climatic niche change explain patterns of diversification among frog families. *American Naturalist* **190**, 29–44.

MOLINA-HENAO, Y. F., GUERRERO-CHACÓN, A. L. & JARAMILLO, M. A. (2016). Ecological and geographic dimensions of diversification in *Piper* subgenus *Ottonia*: a lineage of Neotropical rainforest shrubs. *Systematic Botany* **41**, 253–262.

MOON, C. D., CRAVEN, K. D., LEUCHTMANN, A., CLEMENT, S. L. & SCHARDL, C. L. (2004). Prevalence of interspecific hybrids amongst asexual fungal endophytes of grasses. *Molecular Ecology* **13**, 1455–1467.

MORA, C., TITTENSOR, D. P., ADL, S., SIMPSON, A. G. B. & WORM, B. (2011). How many species are there on earth and in the ocean? *PLoS Biology* **9**, e1001127.

MORAN, N. A., MUNSON, M. A., BAUMANN, P. & ISHIKAWA, H. (1993). A molecular clock in endosymbiotic bacteria is calibrated using the insect hosts. *Proceedings of the Royal Society B: Biological Sciences* **253**, 167–171.

MORRIS, C. E. & MOURY, B. (2019). Revisiting the concept of host range of plant pathogens. *Annual Review of Phytopathology* **57**, 63–90.

*MOURA, C. J., CUNHA, M. R., PORTEIRO, F. M. & ROGERS, A. D. (2011a). The use of the DNA barcode gene 16S mRNA for the clarification of taxonomic problems within the family Sertulariidae (Cnidaria, Hydrozoa). *Zoologica Scripta* **40**, 520–537.

*MOURA, C. J., CUNHA, M. R., PORTEIRO, F. M., YESSON, C. & ROGERS, A. D. (2011b). Evolution of *Nemertesia* hydroids (Cnidaria: Hydrozoa, Plumulariidae) from the shallow and deep waters of the NE Atlantic and western Mediterranean. *Zoologica Scripta* **41**, 79–96.

*MULLEN, S. P. (2006). Wing pattern evolution and the origins of mimicry among North American admiral butterflies (Nymphalidae: *Limenitis*). *Molecular Phylogenetics and Evolution* **39**, 747–758.

MULLEN, S. P. & SHAW, K. L. (2014). Insect speciation rules: unifying concepts in speciation research. *Annual Review of Entomology* **59**, 339–361.

*MULLEN, S. P., DOPMAN, E. B. & HARRISON, R. G. (2008). Hybrid zone origins, species boundaries, and the evolution of wing pattern diversity in a polytypic species complex of North American admiral butterflies (Nymphalidae: *Limenitis*). *Evolution* **62**, 1400–1417.

*MURICY, G., SOLÉ-CAVA, A. M., THORPE, J. P. & BOURY-ESNAULT, N. (1996). Genetic evidence for extensive cryptic speciation in the subtidal sponge *Plakina trilopha* (Porifera: Demospongiae: Homoscleromorpha) from the Western Mediterranean. *Marine Ecology Progress Series* **138**, 181–187.

*MUTHS, D., DAVOULT, D., GENTIL, F. & JOLLIVET, D. (2006). Incomplete cryptic speciation between intertidal and subtidal morphs of *Acrocnida brachiata* (Echinodermata: Ophiuroidea) in the Northeast Atlantic. *Molecular Ecology* **15**, 3303–3318.

*NAKANO, S. (1985). Effect of interspecific mating on female fitness in closely related ladybirds (Henosepilachna). *Kontyû* **53**, 112–119.

*NAKANO, T. & OZAWA, T. (2004). Phylogeny and historical biogeography of limpets of the order patellogastropoda based on mitochondrial DNA sequences. *Journal of Molluscan Studies* **70**, 31–41.

*NAKANO, T., MARSHALL, B. A., KENNEDY, M. & SPENCER, H. G. (2009). The phylogeny and taxonomy of New Zealand *Notoacmea* and *Patelloida* species (Mollusca: Patellogastropoda: Lottiidae) inferred from DNA sequences. *Molluscan Research* **29**, 33–59.

*NATTIER, R., GRANDCOLAS, P., ELIAS, M., DESUTTER-GRANDCOLAS, L., JOURDAN, H., COULOUZ, A. & ROBILLARD, T. (2012). Secondary sympatry caused by range expansion informs on the dynamics of microendemism in a biodiversity hotspot. *PLoS One* **7**, 1–9.

*NAUGHTON, K. M., O'HARA, T. D., APPLETON, B. & GARDNER, M. G. (2014). Sympatric cryptic species in the crinoid genus *Cenolia* (Echinodermata: Crinoidea:

Comasteridae) delineated by sequence and microsatellite markers. *Molecular Phylogenetics and Evolution* **78**, 160–171.

Navaud, O., Barbacci, A., Taylor, A., Clarkson, J. P. & Raffaele, A. (2018). Shifts in diversification rates and host jump frequencies shaped the diversity of host range among Sclerotiniaceae fungal plant pathogens. *Molecular Ecology* **27**, 1309–1323.

*Nichols, S. A. & Barnes, P. A. (2005). A molecular phylogeny and historical biogeography of the marine sponge genus *Placospongia* (phylum Porifera) indicate low dispersal capabilities and widespread crypsis. *Journal of Experimental Marine Biology and Ecology* **323**, 1–15.

Nishiguchi, M. K., Ruby, E. G. & McFall-Ngai, M. J. (1998). Competitive dominance among strains of luminous bacteria provides an unusual form of evidence for parallel evolution in sepiolid squid-vibrio symbioses. *Applied and Environmental Microbiology* **64**, 3209–3213.

*Nishikawa, T., Oohara, I., Saitoh, K., Shigenobu, Y., Hasegawa, N., Kanamori, M., Baba, K., Turon, X. & Bishop, J. D. D. (2014). Molecular and morphological discrimination between an invasive ascidian, *Ascidiella aspersa*, and its congener *A. scabra* (Urochordata: Ascidiacea). *Zoological Science* **31**, 180–185.

Niwa, K., Kobiyama, A. & Sakamoto, T. (2010). Interspecific hybridization in the haploid blade-forming marine crop *Porphyra* (Bangiales, Rhodophyta): occurrence of allodiploidy in surviving F_1 gametophytic blades. *Journal of Phycology* **46**, 693–702.

Noda, S., Kitade, O., Inoue, T., Kawai, M., Kanuka, M., Hiroshima, K., Hongoh, Y., Constantino, R., Uys, V., Zhong, J., Kudo, T. & Ohkuma, M. (2007). Cospeciation in the triplex symbiosis of termite gut protists (*Pseudotrichonympha* spp.), their hosts, and their bacterial endosymbionts. *Molecular Ecology* **16**, 1257–1266.

*Nohara, M., Nishida, M., Manthacitra, V. & Nishikawa, T. (2004). Ancient phylogenetic separation between Pacific and Atlantic cephalochordates as revealed by mitochondrial genome analyses. *Zoological Society of Japan* **21**, 203–210.

*Nosil, P. (2009). Adaptive population divergence in cryptic color-pattern following a reduction in gene flow. *Evolution* **63**, 1902–1912.

Nosil, P. (2012). *Ecological Speciation*. Oxford University Press, New York.

*Nosil, P., Crespi, B. J. & Sandoval, C. P. (2002). Host-plant adaptation drives the parallel evolution of reproductive isolation. *Nature* **417**, 440–443.

*Nosil, P., Gompert, Z., Farkas, T., Comeault, A., Feder, J. L., Buerkle, C. A. & Parchman, T. L. (2012). Genomic consequences of multiple speciation processes in a stick insect. *Proceedings of the Royal Society of London B: Biological Sciences* **279**, 5058–5065.

*Nosil, P., Vines, T. H. & Funk, D. J. (2005). Reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution* **59**, 705–719.

*Nyman, T., Vikberg, V., Smith, D. R. & Boevé, J.-L. (2010). How common is ecological speciation in plant-feeding insects? A 'higher' Nematinae perspective. *BMC Evolutionary Biology* **10**, 266.

Ochman, H., Lawrence, J. G. & Groisman, E. A. (2000). Lateral gene transfer and the nature of bacterial innovation. *Nature* **405**, 299–305.

O'Donnell, K., Sink, S., Libeskind-Hadas, R., Hulcr, J., Kasson, M. T., Ploetz, R. C., Carillo, D., Campbell, A., Duncan, R. E., Liyanage, P. N. H., Eskalen, A., Na, F., Geiser, D. M., Bateman, C., Freeman, S., et al. (2015). Discordant phylogenies suggest repeated host shifts in the *Fusarium-Euwallacea* ambrosia beetle mutualism. *Fungal Genetics and Biology* **82**, 277–290.

*O'Hara, T. D., Smith, P. J., Mills, V. S., Smirnov, I. & Steinke, D. (2013). Biogeographical and phylogeographical relationships of the bathyal ophiuroid fauna of the Macquarie ridge, Southern Ocean. *Polar Biology* **36**, 321–333.

*O'Loughlin, P. M., Paulay, G., Davey, N. & Michonneau, F. (2011). The Antarctic region as a marine biodiversity hotspot for echinoderms: diversity and diversification of sea cucumbers. *Deep Sea Research Part II: Topical Studies in Oceanography* **58**, 264–275.

*O'Loughlin, P. M., Waters, J. M. & Roy, M. S. (2003). A molecular and morphological review of the asterinid, *Patiriella gunnii* (Gray) (Echinodermata: Asteroidea). *Memoirs of Museum Victoria* **60**, 181–195.

*Oh, K. P. & Shaw, K. L. (2013). Multivariate sexual selection in a rapidly evolving speciation phenotype. *Proceedings of the Royal Society of London B: Biological Sciences* **280**, 20130482.

*Oh, K. P., Fergus, D. J., Grace, J. L. & Shaw, K. L. (2012). Interspecific genetics of speciation phenotypes: song and preference coevolution in Hawaiian crickets. *Journal of Evolutionary Biology* **25**, 1500–1512.

*Ohki, S., Kowalski, R. K., Kitanobo, S. & Morita, M. (2015). Changes in spawning time led to the speciation of the broadcast spawning corals *Acropora digitifera* and the cryptic species *Acropora sp.* 1 with similar gamete recognition systems. *Coral Reefs* **34**, 1189–1198.

*Ohshima, I. (2008). Host race formation in the leaf-mining moth *Acrocercops transecta* (Lepidoptera: Gracillariidae). *Biological Journal of the Linnean Society* **93**, 135–145.

*Otte, D. (1994). *The Crickets of Hawaii: Origin, Systematics and Evolution*. Academy of Natural Sciences, Philadelphia.

*Ozawa, T., Kohler, F., Reid, D. G. & Glaubrech, M. (2009). Tethyan relicts on continental coastlines of the northwestern Pacific Ocean and Australasia: molecular phylogeny and fossil record of batillariid gastropods (Caenogastropoda, Cerithioidea). *Zoologica Scripta* **38**, 503–525.

*Page, T. J. & Linse, K. (2002). More evidence of speciation and dispersal across the Antarctic polar front through molecular systematics of Southern Ocean *Limatula* (Bivalvia: Limidae). *Polar Biology* **25**, 818–826.

Palumbi, S. R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annual Review of Ecology and Systematics* **25**, 547–572.

Palumbi, S. R. & Lessios, H. A. (2005). Evolutionary animation: how do molecular phylogenies compare to Mayr's reconstruction of speciation patterns in the sea? *Proceedings of the National Academy of Sciences of the United States of America* **102**, 6566–6572.

*Pappers, S. M., van der Velde, G. & Ouborg, N. J. (2002a). Host preference and larval performance suggest host race formation in *Galerucella nymphaeae*. *Oecologia* **130**, 433–440.

*Pappers, S. M., van der Velde, G., Ouborg, N. J. & van Groenendael, J. M. (2002b). Genetically based polymorphisms in morphology and life history associated with putative host races of the water lily leaf beetle, *Galerucella nymphaeae*. *Evolution* **56**, 1610–1621.

Parent, C. E. & Crespi, B. J. (2006). Sequential colonization and diversification of Galapagos endemic land snail genus *Bulimulus* (Gastropoda, Stylommatophora). *Evolution* **60**, 2311–2328.

*Pashley, D. P., Johnson, S. J. & Sparks, A. N. (1985). Genetic population-structure of migratory moths: the fall armyworm (Lepidoptera, Noctuidae). *Annals of the Entomological Society of America* **78**, 756–762.

Pawlowski, J., Audic, S., Adl, S., Bass, D., Belbahri, L., Berney, C., Bowser, S. S., Cepicka, I., Decelle, J., Dunthorun, M., Fiore-Donno, A. M., Gile, G. H., Holzmann, M., Jahn, R., Jirku, M., et al. (2012). CBOL Protist working group: barcoding eukaryotic richness beyond the animal, plant, and fungal kingdoms. *PLoS Biology* **10**, e1001419.

Peacock, L., Ferris, V., Bailey, M. & Gibson, W. (2014). Mating compatibility in the parasitic protist *Trypanosoma brucei*. *Parasites and Vectors* **7**, 78.

Peakall, R. & Whitehead, M. R. (2014). Floral odour chemistry defines species boundaries and underpins strong reproductive isolation in sexually deceptive orchids. *Annals of Botany* **113**, 341–355.

*Peccoud, J., Ollivier, A., Plantegenest, M. & Simon, J.-C. (2009). A continuum of genetic divergence from sympatric host races to species in the pea aphid complex. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 7495–7500.

Peever, T. L. (2007). Role of host specificity in the speciation of *Ascochyta* pathogens of cool season food legumes. In *Ascochyta Blights of Grain Legumes* (eds B. Tivoli, A. Baranger, F. J. Muehlbauer and B. M. Cooke), pp. 119–126. Springer International Publishing, Cham.

*Peever, T. L., Barve, M. P., Stone, L. J. & Kaiser, W. J. (2007). Evolutionary relationships among *Ascochyta* species infecting wild and cultivated hosts in the legume tribes Cicereae and Vicieae. *Mycologia* **99**, 59–77.

*Pennetier, C., Warren, B., Dabire, K. R., Russell, I. J. & Gibson, G. (2010). "Singing on the wing" as a mechanism for species recognition in the malarial mosquito *Anopheles gambiae*. *Current Biology* **20**, 131–136.

*Pérez-Portela, R. & Turon, X. (2008). Phylogenetic relationships of the Clavelinidae and Pycnoclavellidae (Ascidiacea) inferred from mtDNA data. *Invertebrate Biology* **127**, 108–120.

*Pérez-Portela, R., Almada, V. & Turon, X. (2012). Cryptic speciation and genetic structure of widely distributed brittle stars (Ophiuroidea) in Europe. *Zoologica Scripta* **42**, 151–169.

*Pérez-Portela, R., Villamor, A. & Almada, V. (2010). Phylogeography of the sea star *Marthasterias glacialis* (Asteroidea, Echinodermata): deep genetic divergence between mitochondrial lineages in the north-western Mediterranean. *Marine Biology* **157**, 2015–2028.

Perret, M., Chautems, A., Spichiger, R., Barraclough, T. G. & Savolainen, V. (2007). The geographical pattern of speciation and floral diversification in the Neotropics: the tribe Sinningieae (Gesneriaceae) as a case study. *Evolution* **61**, 1641–1660.

Pereyra, R. T., Bergstrom, L., Kautskly, L. & Johanneson, K. (2009). Rapid speciation in a newly opened postglacial marine environment, the Baltic Sea. *BMC Evolutionary Biology* **9**, 70.

Peterson, K. R., Pfister, D. H. & Bell, C. D. (2010). Cophylogeny and biogeography of the fungal parasite *Cyttaria* and its host *Nothofagus*, southern beech. *Mycologia* **102**, 1417–1425.

*Peterson, S. W., Ito, Y., Horn, B. W. & Goto, T. (2001). *Aspergillus bombycis*, a new aflatoxigenic species and genetic variation in its sibling species, *A. nominus*. *Mycologia* **93**, 689–703.

Phillimore, A. B., Orme, C. D. L., Thomas, G. H., Blackburn, T. M., Bennett, P. M., Gaston, K. J. & Owens, I. P. (2008). Sympatric speciation in birds is rare: insights from range data and simulations. *American Naturalist* **171**, 646–657.

*Pitteloud, C., Arrigo, N., Suchan, T., Mastretta-Yanes, A., Vila, R., Dinca, V., Hernández-Roldán, J., Brockmann, E., Chittaro, Y., Kleckova, I., Fumagalli, L., Buerki, S., Pellisier, L. & Alvarez, N. (2017). Climatic niche evolution is faster in sympatric than allopatric lineages of the butterfly genus *Pyrgus*. *Proceedings of the Royal Society B: Biological Sciences* **284**, 20170208.

*Platt, A. P. (1975). Monomorphic mimicry in Nearctic *Limenitis* butterflies: experimental hybridization of the *L. arthemis-astyanax* complex with *L. archippus*. *Evolution* **29**, 120–141.

*Platt, A. P. & Brower, L. P. (1968). Mimetic versus disruptive coloration in intergrading populations of *Limenitis arthemis* and *astyanax* butterflies. *Evolution* **22**, 699–718.

Poff, K. E., Stever, H., Reil, J. B., Seabourn, P., Ching, A. J., Aoki, S., Logan, M., Michalski, J. R., Santamaria, J., Adams, J. W., Eiben, J. A., Yew, J. Y., Ewing, C. P., Magnacca, K. N. & Bennett, G. M. (2017). The native Hawaiian insect microbiome initiative: a critical perspective for Hawaiian insect evolution. *Insects* **8**, 130.

Pogson, G. H. (2016). Studying the genetic basis of speciation in high gene flow marine invertebrates. *Current Zoology* **62**, 643–653.

*Poliseno, A. (2016a). Historical biogeography and mitogenomics of two endemic Mediterranean gorgonians (Holaxonia, Plexauridae). In: Speciation, evolution and phylogeny of some shallow-water octocorals (Cnidaria: Anthozoa). PhD Dissertation, Ludwig-Maximilians-Universitat Munchen.

*Poliseno, A. (2016b). Species delimitation and phylogeny of the tropical eastern Pacific gorgonian *Pacifigorgia* using single nucleotide polymorphisms (SNPs). In: Speciation, evolution and phylogeny of some shallow-water octocorals (Cnidaria: Anthozoa). PhD Dissertation, Ludwig-Maximilians-Universitat Munchen.

Polz, M. F., Alm, E. J. & Hanage, W. P. (2013). Horizontal gene transfer and the evolution of bacterial and archaeal population structure. *Trends in Genetics* **29**, 170–175.

*Pöppe, J., Sutcliffe, P., Hooper, J. N., Wörheide, G. & Erpenbeck, D. (2010). COI barcoding reveals new clades and radiation patterns of Pacific sponges of the family Irciniidae (Demospongiae: Dictyoceratida). *PLoS One* **5**, e9950.

*Postaire, B., Bruggemann, J. H., Magalon, H. & Faure, B. (2014). Evolutionary dynamics in the southwest Indian Ocean marine biodiversity hotspot: a perspective from the rocky shore gastropod genus *Nerita*. *PLoS One* **9**, 1–11.

*Postaire, B., Magalon, H., Bourmaud, C. A. F. & Bruggemann, J. H. (2016). Molecular species delimitation methods and population genetics data reveal extensive lineage diversity and cryptic species in Aglaopheniidae (Hydrozoa). *Molecular Phylogenetics and Evolution* **105**, 36–49.

*Postaire, B., Magalon, H., Bourmaud, C. A. F., Bonnet, N. G. & Bruggemann, J. E. (2015). Phylogenetic relationships within Aglaopheniidae (Cnidaria, Hydrozoa) reveal unexpected generic diversity. *Zoologica Scripta* **45**, 103–114.

Poulíeková, A., Mazalová, P., Vasut, R. J., Šarhnová, P., Neustupa, J. & Škaloud, P. (2014). DNA content variation and its significance in the evolution of the genus *Micrasterias* (Desmidiales, Streptophyta). *PLoS One* **9**, e86247.

*Powell, T., Linn, C. E., Cha, D. H. & Feder, J. L. (2012). On the scent of standing variation for speciation: behavioral evidence for native sympatric host races of *Rhagoletis pomonella* (Diptera: Tephritidae) in the southern United States. *Evolution* **66**, 2739–2756.

*Prada, C., Schizas, N. V. & Yoshioka, P. M. (2008). Phenotypic plasticity or speciation? A case from a clonal marine organism. *BMC Evolutionary Biology* **8**, 47.

Presgraves, D. C. (2010). The molecular evolutionary basis of species formation. *Nature Reviews Genetics* **11**, 175–180.

Price, J. P. & Wagner, W. L. (2004). Speciation in Hawaiian angiosperm lineages: cause, consequence, and mode. *Evolution* **58**, 2185–2200.

Price, T. D. (2008). *Speciation in Birds*. Sinauer Associates, Sunderland.

*Pringle, A., Baker, D. M., Platt, J. L., Wares, J. P., Latgé, J. P. & Taylor, J. W. (2005). Cryptic speciation in the cosmopolitan and clonal human pathogenic fungus *Aspergillus fumigatus*. *Evolution* **59**, 1886–1899.

*Prowell, D. P., McMichael, M. & Silvain, J. F. (2004). Multilocus genetic analysis of host use, introgression, and speciation in host strains of fall armyworm (Lepidoptera: Noctuidae). *Annals of the Entomological Society of America* **97**, 1034–1044.

Puebla, O. (2009). Ecological speciation in marine v. freshwater fishes. *Journal of Fish Biology* **75**, 960–996.

Puritz, J. B., Keever, C. C., Addison, J. A., Byrne, M., Hart, M. W., Grosberg, R. K. & Toonen, R. J. (2012). Extraordinarily rapid life-history divergence between *Cryptasterina* sea star species. *Proceedings of the Royal Society B: Biological Sciences* **279**, 3914–3922.

*Puslednik, L., Ponder, W. F., Dowton, M. & Davis, A. R. (2009). Examining the phylogeny of the Australasian Lymnaeidae (Heterobranchia: Pulmonata: Gastropoda) using mitochondrial, nuclear and morphological markers. *Molecular Phylogenetics and Evolution* **52**, 643–659.

Queloz, V., Grunig, C. R., Berndt, R., Kowalski, T., Sieber, T. N. & Holdenrieder, O. (2011). Cryptic speciation in *Hymenoscyphus albidus*. *Forest Pathology* **41**, 133–142.

Quenouille, B., Hubert, N., Bermingham, E. & Planes, S. (2011). Speciation in tropical seas: allopatry followed by range change. *Molecular Phylogenetics and Evolution* **58**, 546–552.

Rahman, M. A., Uehara, T. & Pearse, J. S. (2001). Hybrids of two closely related tropical sea urchins (genus *Echinometra*): evidence against postzygotic isolating mechanisms. *Biology Bulletin* **200**, 97–106.

Ramjee & Sarma, Y. S. R. K. (1971). Some observations on the morphology and cytology of Indian Charophyta. *Hydrobiologia* **37**, 367–382.

Ramiro, R. S., Khan, S. M., Franke-Fayard, B., Janse, C. J., Obbard, D. J. & Reece, S. E. (2015). Hybridization and prezygotic reproductive barriers in *Plasmodium*. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20143027.

Randler, C. (2008). Mating patterns in avian hybrid zones—a meta-analysis and review. *Ardea* **96**, 73–80.

Refrégier, G., Le Gac, M., JabbourA, F., Widmer, A., Shykoff, J. A., Yockteng, R., Hood, M. E. & Giraud, T. (2008). Cophylogeny of the anther smut fungi and their caryophyllaceous hosts: prevalence of host shifts and importance of delimiting parasite species for inferring cospeciation. *BMC Evolutionary Biology* **8**, 100.

*Reid, D. G., Claremont, M., Smith, L., Shamoto, M., Glaubrecht, M. & Ozawa, T. (2013). Mosaics in the mangroves: allopatric diversification of tree-climbing mudwhelks (Gastropoda: Potamididae: *Cerithidea*) in the Indo-West Pacific. *Biological Journal of the Linnean Society* **110**, 564–580.

*Reid, D., Dyall, P., Lozouet, P., Glaubrecht, M. & Williams, S. (2008). Mudwhelks and mangroves: the evolutionary history of an ecological association (Gastropoda: Potamididae). *Molecular Phylogenetics and Evolution* **47**, 680–699.

*Reidenbach, K. R., Neafsey, D. E., Costantini, C., Sagnon, N. F., Simard, F., Ragland, G. J., Egan, S. P., Feder, J. L., Muskavitch, M. A. T. & Besansky, N. J. (2012). Patterns of genomic differentiation between ecologically differentiated M and S forms of *Anopheles gambiae* in West and Central Africa. *Genome Biology and Evolution* **4**, 1202–1212.

*Reimer, J. D., Takishita, K., Ono, S. & Maruyama, T. (2007). Diversity and evolution in the zoanthid genus *Palythoa* (Cnidaria: Hexacorallia) based on nuclear ITS-rDNA. *Coral Reefs* **26**, 399–410.

Reno, M. L., Ni, L., Held, C., Fields, C. J., Burke, P. V. & Whitaker, R. J. (2009). Biogeography of the *Sulfolobus islandicus* pan-genome. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 8605–8610.

Restrepo, S., Tabimo, J. F., Mideros, M. F., Grunwald, N. J. & Matute, D. R. (2014). Speciation in fungal and oomycete plant pathogens. *Annual Review of Phytopathology* **52**, 289–316.

Retchless, A. C. & Lawrence, J. G. (2012). Ecological adaptation in bacteria: speciation driven by codon selection. *Molecular Biology and Evolution* **29**, 3669–3683.

*Reveillaud, J., Remerie, T., van Soest, R., Erpenbeck, D., Cárdenas, P., Derycke, S., Xavier, J. R., Rigaux, A. & Vanreusel, A. (2010). Species boundaries and phylogenetic relationships between Atlanto-Mediterranean shallow-water and deep-sea coral associated *Hexadella* species (Porifera, Ianthellidae). *Molecular Phylogenetics and Evolution* **56**, 104–114.

*Reveillaud, J., van Soest, R., Derycke, S., Picton, B., Rigaux, A. & Vanreusel, A. (2011). Phylogenetic relationships among NE Atlantic *Plocamionida* Topsent (1927) (Porifera, Poecilosclerida): under-estimated diversity in reef ecosystems. *PLoS One* **6**, e16533.

*Rhodes, B. C., Blair, C. P., Takahashi, M. K. & Abrahamson, W. G. (2012). The role of olfactory cues in the sequential radiation of a gall-boring beetle, *Mordellistena convicta*. *Ecological Entomology* **37**, 500–507.

Richards, P. M., Morii, Y., Kimura, K., Hirano, T., Chiba, S. & Davison, A. (2017). Single-gene speciation: mating and gene flow between mirror-image snails. *Evolution Letters* **1**, 282–291.

Richmond, J. Q., Jockusch, E. L. & Latimer, A. M. (2011). Mechanical reproductive isolation facilitates parallel speciation in western North American scincid lizards. *American Naturalist* **178**, 320–332.

Ricklefs, R. E., Fallon, S. M. & Bermingham, E. (2004). Evolutionary relationships, cospeciation, and host switching in avian malaria parasites. *Systematic Biology* **53**, 111–119.

*Ries, L. & Mullen, S. P. (2008). A rare model limits the distribution of its more common mimic: a twist on frequency-dependent Batesian mimicry. *Evolution* **62**, 1798–1803.

Rieseberg, L. H. & Willis, J. H. (2007). Plant speciation. *Science* **317**, 910–914.

*Riginos, C. & Cunningham, C. W. (2005). Invited review: local adaptation and species segregation in two mussel (*Mytilus edulis* × *Mytilus trossulus*) hybrid zones. *Molecular Ecology* **14**, 381–400.

Ritchie, M. G. (2007). Sexual selection and speciation. *Annual Review of Ecology Evolution and Systematics* **38**, 79–102.

*Ritchie, M. G., Butlin, R. K. & Hewitt, G. M. (1989). Assortative mating across a hybrid zone in *Chorthippus parallelus* (Orthoptera: Acrididae). *Journal of Evolutionary Biology* 2, 339–352.

*Ritchie, M. G., Butlin, R. K. & Hewitt, G. M. (2008). Fitness consequences of potential assortative mating inside and outside a hybrid zone in *Chorthippus parallelus* (Orthoptera: Acrididae): implications for reinforcement and sexual selection theory. *Biological Journal of the Linnean Society* 45, 219–234.

*Rodriguez, R. L., Sullivan, L. E. & Cocroft, R. B. (2004). Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Homoptera: Membracidae). *Evolution* 58, 571–578.

*Rodriguez, R. L., Ramaswamy, K. & Cocroft, R. B. (2006). Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. *Proceedings of the Royal Society B: Biological Sciences* 273, 2585–2593.

Rogacheva, A. V., Mironov, A. N., Minin, K. V. & Gebruk, A. V. (2013). Morphological evidence of depth-related speciation in deep-sea Arctic echinoderms. *Invertebrate Zoology* 10, 143–166.

*Ross, C. L. & Harrison, R. G. (2002). A fine-scale spatial analysis of the mosaic hybrid zone between *Gryllus firmus* and *Gryllus pennsylvanicus*. *Evolution* 56, 2296–2312.

Rosser, N., Kozak, K. M., Phillimore, A. B. & Mallet, J. (2015). Extensive range overlap between heliconiine sister species: evidence for sympatric speciation in butterflies? *BMC Evolutionary Biology* 15, 125.

Rundell, R. J. (2008). Cryptic diversity, molecular phylogeny and biogeography of the rock- and leaf litter-dwelling land snails of Belau (Republic of Palau, Oceania). *Philosophical Transactions of the Royal Society B: Biological Sciences* 363, 3401–3412.

*Russo, C. A. M., Solé-Cava, A. M. & Thorpe, J. P. (1994). Population structure and genetic variation in two tropical sea anemones (Cnidaria, Actinidae) with different reproductive strategies. *Marine Biology* 119, 267–276.

Rutzler, K., Duran, S. & Piantoni, C. (2007). Adaptation of reef and mangrove sponges to stress: evidence for ecological speciation exemplified by *Chondrilla caribensis* new species (Demospongiae, Chondrosida). *Marine Ecology* 28, 95–111.

*Saitoh, S. & Katakura, H. (1991). Strictly parapatric distribution of flightless leaf beetles of the *Chrysolina angusticollis* species complex (Coleoptera, Chrysomelidae) in the vicinity of Sapporo, northern Japan. *Biological Journal of the Linnean Society* 57, 371–384.

*Saitoh, S., Miyai, S. & Katakura, H. (2008). Geographical variation and diversification in the flightless leaf beetles of the *Chrysolina angusticollis* species complex (Chrysomelidae, Coleoptera) in northern Japan. *Biological Journal of the Linnean Society* 93, 557–578.

*Sales, J. B. D. L., Rodrigues-Filho, L. F. d. S., do Ferreira, Y. S., Carneiro, J., Asp, N. E., Shaw, P. W., Haimovici, M., Markaida, U., Ready, J., Schneider, H. & Sampaio, I. (2017). Divergence of cryptic species of *Doryteuthis plei* Blainville, 1823 (Loliginidae, Cephalopoda) in the Western Atlantic Ocean is associated with the formation of the Caribbean Sea. *Molecular Phylogenetics and Evolution* 106, 44–54.

Sanders, J. G., Powell, S., Kronauer, D. J. C., Vasconcelos, H. L., Frederickson, M. E. & Pierce, N. E. (2014). Stability and phylogenetic correlation in gut microbiota: lessons from ants and apes. *Molecular Ecology* 23, 1268–1283.

*Sanford, M. R., Demirci, B., Marsden, C. D., Lee, Y., Cornel, A. J. & Lanzaro, G. C. (2011). Morphological differentiation may mediate mate-choice between incipient species of *Anopheles gambiae* s.s. *PLoS One* 6, e27920.

Sargent, R. D. (2004). Floral symmetry affects speciation rates in angiosperms. *Proceedings of the Royal Society B: Biological Sciences* 271, 603–608.

Sauer, C., Stackebrandt, E., Gadau, J., Holldobler, B. & Gross, R. (2000). Systematic relationships and cospeciation of bacterial endosymbionts and their carpenter ant host species: proposal of the new taxon *Candidatus* Blochmannia gen. nov. *International Journal of Systematic and Evolutionary Microbiology* 50, 1877–1886.

*Savage, W. K. & Mullen, S. P. (2009). A single origin of Batesian mimicry among hybridizing populations of admiral butterflies (*Limenitis arthemis*) rejects an evolutionary reversion to the ancestral phenotype. *Proceedings of the Royal Society B: Biological Sciences* 276, 2557–2565.

*Savolainen, R. & Vepsalainen, K. (2003). Sympatric speciation through intraspecific social parasitism. *Proceedings of the National Academy of Sciences of the United States of America* 100, 7169–7174.

*Schama, R., Solé-Cava, A. M. & Thorpe, J. P. (2005). Genetic divergence between east and West Atlantic populations of *Actinia* spp. sea anemones (Cnidaria: Actiniidae). *Marine Biology* 146, 435–443.

Schemske, D. W. & Bradshaw, H. D. (1999). Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences of the United States of America* 96, 11910–11915.

Schluter, D. (2009). Evidence for ecological speciation and its alternative. *Science* 323, 737–741.

Schmutzer, M. & Barraclough, T. G. (2019). The role of recombination, niche-specific gene pools and flexible genomes in the ecological speciation of bacteria. *Ecology and Evolution* 9, 4544–4556.

Schnitzler, J., Graham, C. H., Dormann, C. F., Schifers, K. & Linder, H. P. (2012). Climatic niche evolution and species diversifcation in the Cape flora, South Africa. *Journal of Biogeography* 39, 2201–2211.

Scholl, J. P. & Wiens, J. J. (2016). Diversification rates and species richness across the Tree of Life. *Proceedings of the Royal Society of London, B: Biological Sciences* 283, 20161335.

Schroth, W., Jarms, G., Streit, B. & Schierwater, B. (2002). Speciation and phylogeography in the cosmopolitan marine moon jelly, *Aurelia* sp. *BMC Evolutionary Biology* 2, 1.

*Schuchert, P. (2014). High genetic diversity in the hydroid *Plumularia setacea*: a multitude of cryptic species or extensive population subdivision? *Molecular Phylogenetic and Evolution* 76, 1–9.

Schumer, M., Rosenthal, G. G. & Andolfatto, P. (2014). How common is homoploid hybrid speciation? *Evolution* 68, 1553–1560.

*Schwentner, M. & Bosch, T. C. G. (2015). Revisiting the age, evolutionary history and species level diversity of the genus *Hydra* (Cnidaria: Hydrozoa). *Molecular Phylogenetics and Evolution* 91, 41–55.

Seears, H. A., Darling, K. F. & Wade, C. M. (2012). Ecological partitioning and diversity in tropical planktonic foraminifera. *BMC Evolutionary Biology* 12, 54.

Seehausen, O., Butlin, R. K., Keller, I., Wagner, C. E., Boughman, J. W., Hohenlohe, P. A., Peichel, C. L., Saetre, G.-P., Bank, C., Brannstrom, A., Brelsford, A., Clarkson, C. S., Eroukhmanoff, F., Feder, J. L., Fischer, M. C., et al. (2014). Genomics and the origin of species. *Nature Reviews Genetics* 15, 176–192.

Seehausen, O. & Wagner, C. E. (2014). Speciation in freshwater fishes. *Annual Review of Ecology Evolution and Systematics* 45, 621–651.

Seehausen, O., van Alphen, J. J. M. & Witte, F. (1997). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277, 1808–1811.

*Sérusiaux, E., Villarreal, A., C, J., Wheeler, T. & Goffinet, B. (2011). Recent origin, active speciation and dispersal for the lichen genus *Nephroma* (Peltigerales) in Macaronesia. *Journal of Biogeography* 38, 1138–1151.

*Sezer, M. & Butlin, R. K. (1998). The genetic basis of host plant adaptation in the brown planthopper (*Nilaparvata lugens*). *Heredity* 80, 499–508.

Shafer, A. B. A., Williams, G. R., Shutler, D., Rogers, R. E. L. & Stewart, D. T. (2009). Cophylogeny of *Nosema* (Microsporidia: Nosematidae) and bees (Hymenoptera: Apidae) suggests both cospeciation and a host-switch. *Journal of Parasitology* 95, 198–203.

Shapiro, B. J., Friedman, J., Cordero, O. X., Preheim, S. P., Timberlake, S. C., Szabó, G., Polz, M. F. & Alm, E. J. (2012). Population genomics of early events in the ecological differentiation of bacteria. *Science* 336, 48–51.

*Shaw, K. L. & Herlihy, D. (2000). Acoustic preference functions and song variability in the Hawaiian cricket *Laupala cerasina*. *Proceedings of the Royal Society of London B: Biological Sciences* 267, 577–584.

Skeels, A. & Cardillo, M. (2019). Reconstructing the geography of speciation from contemporary biodiversity data. *The American Naturalist* 193, 240–255.

*Slippers, B., Fourie, G., Crous, P. W., Coutinho, T. A., Wingfield, B. D., Carnegie, A. J. & Wingfield, M. J. (2004). Speciation and distribution of *Botryosphaeria* spp. on native and introduced *Eucalyptus* trees in Australia and South Africa. *Studies in Mycology* 50, 343–358.

Smadja, C. & Butlin, R. K. (2009). On the scent of speciation: the chemosensory system and its role in premating isolation. *Heredity* 102, 77–97.

*Smadja, C. M., Canback, B., Vitalis, R., Gauthier, M., Ferrari, J., Zhou, J.-J. & Butlin, R. K. (2012). Large-scale candidate gene scan reveals the role of chemoreceptor genes in host plant specialisation and speciation in the pea aphid. *Evolution* 66, 2723–2738.

Sobel, J. M. & Streisfeld, M. A. (2015). Strong premating isolation exclusively drives incipient speciation in *Mimulus aurantiacus*. *Evolution* 69, 447–461.

*Song, X., Gravili, C., Wang, J., Deng, Y., Wang, Y., Fang, L., Lin, H., Wang, S., Zheng, Y. & Lin, J. (2016). A new deep-sea hydroid (Cnidaria: Hydrozoa) from the Bering Sea Basin reveals high genetic relevance to Arctic and adjacent shallow-water species. *Polar Biology* 39, 461–471.

Soria-Carrasco, V., Gompert, Z., Comeault, A. A., Farkas, T. E., Parchman, T. L., Johnston, J. S., Buerkle, C. A., Feder, J. L., Bast, J., Schwander, T., Egan, S. P., Crespi, B. J. & Nosil, P. (2014). Stick insect genomes reveal natural selection's role in parallel speciation. *Science* 344, 738–742.

*Soudi, S., Reinhold, K. & Eengqvist, L. (2016). Ecologically dependent and intrinsic genetic signatures of postzygotic isolation between sympatric host races of the leaf beetle *Lochmaea capreae*. *Evolution* 70, 471–479.

Spaulding, A. W. & von Dohlen, C. D. (2001). Psyllid endosymbionts exhibit patterns of co-speciation with hosts and destabilizing substitutions in ribosomal RNA. *Insect Molecular Biology* 10, 57–67.

*Stampar, S. N., Maronna, M. M., Vermeij, M. J. A., de Silveria, F. L. & Morandini, A. C. (2012). Evolutionary diversification of banded tube-dwelling anemones (Cnidaria; Ceriantharia; *Isarachnanthus*) in the Atlantic Ocean. *PLoS One* 7, e41091.

STEBBINS, G. L. (1950). *Variation and Evolution in Plants*. Columbia University Press, New York.

*STEENKAMP, E. T., WINGFIELD, B. D., DESJARDINS, A. E., MARASAS, W. F. O. & WINGFIELD, M. J. (2002). Cryptic speciation in *Fusarium subglutinans*. *Mycologia* **94**, 1032–1043.

STEENKAMP, E. T., WINGFIELD, M. J., MCTAGGART, A. R. & WINGFIELD, B. D. (2018). Fungal species and their boundaries matter – definitions, mechanisms, and practical implications. *Fungal Biology Reviews* **32**, 104–116.

*STEFANI, F., BENZONI, F., YANG, S. Y., PICHON, M., GALLI, P. & CHEN, C. A. (2011). Comparison of morphological and genetic analyses reveals cryptic divergence and morphological plasticity in *Stylophora* (Cnidaria, Scleractinia). *Coral Reefs* **30**, 1033–1049.

STELKENS, R. B., YOUNG, K. A. & SEEHAUSEN, O. (2009). The accumulation of reproductive incompatibilities in African cichlid fish. *Evolution* **64**, 617–633.

STEPHENS, P. R. & WIENS, J. J. (2003). Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *American Naturalist* **161**, 112–128.

*STEWART, J. E., TIMMER, L. W., LAWRENCE, C. B., PRYOR, B. M. & PEEVER, T. L. (2014). Discord between morphological and phylogenetic species boundaries: incomplete lineage sorting and recombination results in fuzzy species boundaries in an asexual fungal pathogen. *BMC Evolutionary Biology* **14**, 38.

*STIREMAN, J. O. III, NASON, J. D. & HEARD, S. B. (2005). Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. *Evolution* **59**, 2573–2587.

STOCK, A., EDGCOMB, V., ORSI, W., FILKER, S., BREINER, H.-W., YAKIMOV, M. M. & STOECK, T. (2013). Evidence for isolated evolution of deep-sea ciliate communities through geological separation and environmental selection. *BMC Microbiology* **13**, 150.

STREELMAN, J. T. & DANLEY, P. D. (2003). The stages of vertebrate evolutionary radiation. *Trends in Ecology and Evolution* **18**, 126–131.

STUKENBROCK, E. H. (2016). The role of hybridization in the evolution and emergence of new fungal plant pathogens. *Phytopathology* **106**, 104–112.

STUKENBROCK, E. H., JORGENENSEN, F. G., ZALA, M., HANSEN, T. T., MCDONALE, B. A. & SCHIERUP, M. H. (2010). Whole-genome and chromosome evolution associated with host adaptation and speciation of the wheat pathogen *Mycosphaerella graminicola*. *PLoS Genetics* **6**, e1001189.

SVENSSON, E. I. (2012). Non-ecological speciation, niche conservatism and thermal adaptation: how are they connected? *Organisms Diversity and Evolution* **12**, 229–240.

*TARJUELO, I., POSADA, D., CRANDALL, K. A., PASCUAL, M. & TURON, X. (2001). Cryptic species of *Clavelina* (Ascidiacea) in two different habitats: harbours and rocky littoral zones in the northwestern Mediterranean. *Marine Biology* **139**, 455–462.

TARJUELO, I., POSADA, D., CRANDALL, K. A., PASCUAL, M. & TURON, X. (2004). Phylogeography and speciation of colour morphs in the colonial ascidian *Pseudodistoma crucigaster*. *Molecular Ecology* **13**, 3125–3136.

TAYLOR, J. W., JACOBSON, D. J., KROKEN, S., KASUGA, T., GEISER, D. M., HIBBETT, D. S. & FISHER, M. C. (2000). Phylogenetic species recognition and species concepts in Fungi. *Fungal Genetics and Biology* **31**, 21–32.

TAYLOR, J. W., HANN-SODEN, C., BRANCO, S., SYLVAIN, I. & ELLISON, C. E. (2015). Clonal reproduction in fungi. *Proceedings of the National Academy of Sciences of the United States of America* **112**, 8901–8908.

*TEIXEIRA, M. M., THEODORO, R. C., DE CARVALHO, M. J. A., FERNANDES, L., PAES, H. C., HAHN, R. C., MENDOZA, L., BAGAGLI, E., SAN-BLAS, G. & FELIPE, M. S. S. (2009). Phylogenetic analysis reveals a high level of speciation in the *Paracoccidioides* genus. *Molecular Phylogenetics and Evolution* **52**, 273–283.

*TEPPER, C., SQUIERS, L., HAY, C., GORBACH, D., FRIEND, D., BLACK, B., GREENSTEIN, B. & STRYCHAR, K. (2012). Cryptic species: a mismatch between genetics and morphology in *Millepora*. *Marine Sciences* **2**, 57–65.

*TESKE, P. R., RIUS, M., MCQUAID, C. D., STYAN, C. A., PIGGOTT, M. P., BENHISSOUNE, S., FUENTES-GRUNEWALD, C., WALLS, K., PAGE, M., ATTARD, C. R. M., COOKE, G. M., MCCLUSKY, C. F., BANKS, S. C., BARKER, N. P. & BEHEREGARAY, L. B. (2011). "Nested" cryptic diversity in a widespread marine ecosystem engineer: a challenge for detecting biological invasions. *BMC Evolutionary Biology* **11**, 176.

THAO, M. L., MORAN, N. A., ABBOT, P., BRENNAN, E. B., BURCKHARDT, D. H. & BAUMANN, P. (2000). Cospeciation of psyllids and their primary prokaryotic endosymbionts. *Applied and Environmental Microbiology* **66**, 2898–2905.

THAO, M. L., GULLAN, P. J. & BAUMANN, P. (2002). Secondary (gamma-Proteobacteria) endosymbionts infect the primary (beta-Proteobacteria) endosymbionts of mealybugs multiple times and coevolve with their hosts. *Applied and Environmental Microbiology* **68**, 3190–3197.

THINS, M., CHOI, Y. J., KEMEN, E., PLOCH, S., HOLUB, E. B., SHIN, H. D. & JONES, J. D. G. (2009). A new species of *Albugo* parasitic to *Arabidopsis thaliana* reveals new evolutionary patterns in white blister rusts (Albuginaceae). *Persoonia* **22**, 123–128.

*THOMAS, Y., BETHENOD, M.-T., PELOZUELO, L., FREROT, B. & BOURGUET, D. (2003). Genetic isolation between two sympatric host-plant races of the European

corn borer, *Ostrinia nubilalis* Hubner. I. sex pheromone, moth emergence timing, and parasitism. *Evolution* **57**, 261–273.

*THORNHILL, D. J., XIANG, Y., PETTAY, D. T. & ZHONG, M. (2013). Population genetic data of a model symbiotic cnidarian system reveal remarkable symbiotic specificity and vectored introductions across ocean basins. *Molecular Ecology* **22**, 4499–4515.

*THORPE, J. P., RYLAND, J. S., CORNELIUS, P. F. S. & BEARDMORE, J. A. (1992). Genetic divergence between branched and unbranched forms of the thecate hydroid *Aglaophenia pluma*. *Journal of the Marine Biology Association of the United Kingdom* **72**, 887–894.

*TILMON, K. J., WOOD, T. K. & PESEK, J. D. (1998). Genetic variation in performance traits and the potential for host shifts in *Enchenopa binotata* treehoppers (Homoptera: Membracidae). *Annals of the Entomological Society of America* **91**, 397–403.

*TORRES-PRATTS, H., LADO-INSUA, T., RHYNE, A. L., RODRÍGUES-MATOS, L. & SCHIZAS, N. V. (2011). Two distinct, geographically overlapping lineages of the corallimorpharian *Ricordea florida* (Cnidaria: Hexacorallia: Ricordeidae). *Coral Reefs* **30**, 391–396.

TUCKER, R. P. (2013). Horizontal gene transfer in Choanoflagellates. *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution* **320**, 1–9.

*TREGENZA, T., PRITCHARD, V. L. & BUTLIN, R. K. (2000). Patterns of trait divergence between populations of the meadow grasshopper, *Chorthippus parallelus*. *Evolution* **54**, 574–585.

*TREGENZA, T., PRITCHARD, V. L. & BUTLIN, R. K. (2002). The origins of postmating reproductive isolation: testing hypotheses in the grasshopper *Chorthippus parallelus*. *Population Ecology* **44**, 137–144.

*TRIPET, F., TOURE, Y. T., TAYLOR, C. E., NORRIS, D. E., DOLO, G. & LANZARO, G. C. (2001). DNA analysis of transferred sperm reveals significant levels of gene flow between molecular forms of *Anopheles gambiae*. *Molecular Ecology* **10**, 1725–1732.

*TU, T., DAI, C. & JENG, M. (2015). Phylogeny and systematics of deep-sea precious corals (Anthozoa: Octocorallia: Coralliidae). *Molecular Phylogenetics and Evolution* **84**, 173–184.

TURNER, E., JACOBSON, D. J. & TAYLOR, J. W. (2010). Reinforced postmating reproductive isolation barriers in *Neurospora*, an Ascomycete microfungus. *Journal of Evolutionary Biology* **23**, 1642–1656.

*TURNER, L. M. & WILSON, N. G. (2008). Polyphyly across oceans: a molecular phylogeny of the Chromodorididae (Mollusca, Nudibranchia). *Zoologica Scripta* **37**, 23–42.

UESHIMA, R. & ASAMI, T. (2003). Single-gene speciation by left-right reversal—a land-snail species of polyphyletic origin results from chirality constraints on mating. *Nature* **425**, 679–679.

*URAWA, S., FREEMAN, M. A., JOHNSON, S. C., JONES, S. R. M. & YOKOYAMA, H. (2011). Geographical variation in spore morphology, gene sequences and host specificity of *Myxobolus arcticus* (Myxozoa) infecting salmonid nerve tissues. *Diseases of Aquatic Organisms* **96**, 229–237.

*USHER, K. M., SUTTON, D. C., TOZE, S., KUO, J. & FROMONT, J. (2004). Biogeography and phylogeny of *Chondrilla* species (Demospongiae) in Australia. *Marine Ecology Progress Series* **270**, 117–127.

*UTHICKE, S. & BENZIE, J. A. H. (2003). Gene flow and population history in high dispersal marine invertebrates: mitochondrial DNA analysis of *Holothuria nobilis* (Echinodermata: Holothuroidea) populations from the Indo-Pacific. *Molecular Ecology* **12**, 2635–2648.

*UTHICKE, S., PURCELL, S. & BLOCKMANS, B. (2005). Natural hybridization does not dissolve species boundaries in commercially important sea cucumbers. *Biological Journal of the Linnaean Society* **85**, 261–270.

UY, J. A., IRWIN, D. E. & WEBSTER, M. S. (2017). Behavioral isolation and incipient speciation in birds. *Annual Review of Ecology Evolution and Systematics* **49**, 1–24.

*VALDERRAMA, D., ROSSI, A. L., SOLÉ-CAVA, A. M., RAPP, H. T. & KLAUTAU, M. (2009). Revalidation of *Leucetta floridana* (Haeckel, 1872) (Porifera, Calcarea): a widespread species in the tropical western Atlantic. *Zoological Journal of the Linnean Society* **157**, 1–16.

*VAN DER MERWE, N. A., GRYZENHOUT, M., STEENKAMP, E. T., WINGFIELD, B. D. & WINGFIELD, M. J. (2010). Multigene phylogenetic and population differentiation data confirm the existence of a cryptic species within *Chrysoporthe cubensis*. *Fungal Biology* **114**, 966–979.

VAN DER NIET, T. & JOHNSON, S. D. (2009). Patterns of plant speciation in the Cape floristic region. *Molecular Phylogenetics and Evolution* **51**, 85–93.

*VANDEPAS, L. E., OLIVEIRA, L. M., LEE, S. S. C., HIROSE, E., ROCHA, R. M. & SWALLA, B. J. (2015). Biogeography of *Phallusia nigra*: is it really black and white? *The Biological Bulletin* **228**, 52–64.

*VIA, S. (1991). The genetic structure of host plant adaptation in a spatial patchwork: demographic variability among reciprocally transplanted pea aphid clones. *Evolution* **45**, 827–852.

*VIA, S. (1994). *Population Structure and Local Adaptation in a Clonal Herbivore. Ecological Genetics*. Princeton University Press, Princeton.

*VIA, S. (1999). Reproductive isolation between sympatric races of pea aphids. I. Gene flow restriction and habitat choice. *Evolution* **53**, 1446–1457.

*Via, S. & Hawthorne, D. J. (2002). The genetic architecture of ecological specialization: correlated gene effects on host use and habitat choice in pea aphids. *American Naturalist* **159**, S76–S88.

*Via, S. & Hawthorne, D. J. (2005). Back to the future: genetic correlations, adaptation and speciation. *Genetica* **123**, 147–156.

*Via, S., Bouck, A. C. & Skillman, S. (2000). Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. *Evolution* **54**, 1626–1637.

*Vilgalys, R. & Sun, B. L. (1994). Ancient and recent patterns of geographic speciation in the oyster mushroom *Pleurotus* revealed by phylogenetic analysis of ribosomal DNA sequences. *Proceedings of the National Academy of Sciences of the United States of America* **91**, 4599–4603.

*Vincenot, L., Nara, K., Sthultz, C., Labbé, J., Dubois, M. P., Tedersoo, L., Martin, F. & Selosse, M. A. (2012). Extensive gene flow over Europe and possible speciation over Eurasia in the ectomycorrhizal basidiomycete *Laccaria amethystina* complex. *Molecular Ecology* **21**, 281–299.

Vos, M. (2011). A species concept for bacteria based on adaptive divergence. *Trends in Microbiology* **19**, 1–7.

Vulic, M., Lenski, R. E. & Radman, M. (1999). Mutation, recombination, and incipient speciation of bacteria in the laboratory. *Proceedings of the National Academy of Sciences of the United States of America* **96**, 7348–7351.

Wang, I. J., Glor, R. E. & Losos, J. B. (2013). Quantifying the roles of ecology and geography in spatial genetic divergence. *Ecology Letters* **16**, 175–182.

*Wani, R. (2011). Sympatric speciation drove the macroevolution of fossil cephalopods. *Geology* **39**, 1079–1082.

*Wares, J. P. (2001). Biogeography of *Asterias*: North Atlantic climate change and speciation. *The Biological Bulletin* **201**, 95–103.

Warren, D. L., Glor, R. E. & Turelli, M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution* **62**, 2868–2883.

Waser, N. M. & Campbell, D. R. (2004). Ecological speciation in flowering plants. In *Adaptive Speciation*, pp. 264–277 (eds U. Dieckmann, M. Doebeli, J. A. J. Metz and D. Tautz), Cambridge University Press, Cambridge.

Waters, A. P., Higgins, D. G. & McCutchan, T. F. (1991). *Plasmodium falciparum* appears to have arisen as a result of a lateral transfer between avian and human hosts. *Proceedings of the National Academy of Sciences of the United States of America* **88**, 3140–3144.

*Waters, J. & Roy, M. (2003a). Global phylogeography of the fissiparous sea-star genus *Coscinasterias*. *Marine Biology* **142**, 185–191.

*Waters, J. M. & Roy, M. S. (2003b). Marine biogeography of southern Australia: phylogeographical structure in a temperate sea-star. *Journal of Biogeography* **30**, 1787–1796.

*Waters, J. M., O'Loughlin, P. M. & Roy, M. S. (2004). Cladogenesis in a starfish species complex from southern Australia: evidence for vicariant speciation? *Molecular Phylogenetics and Evolution* **32**, 236–245.

*Weber, M. G., Mitko, L., Eltz, T. & Ramírez, S. R. (2016). Macroevolution of perfume signalling in orchid bees. *Ecology Letters* **19**, 1314–1323.

*Webster, N. B., Tdooren, T. J. V. & Schilthuizen, M. (2012). Phylogenetic reconstruction and shell evolution of the Diplommatinidae (Gastropoda: Caenogastropoda). *Molecular Phylogenetics and Evolution* **63**, 625–638.

Wei, N. W., Hsieh, H. J., Dai, C. F., Wallace, C. C., Baird, A. H. & Chen, C. A. (2012). Reproductive isolation among *Acropora* species (Scleractinia: Acroporidae) in a marginal coral assemblage. *Zoological Studies* **51**, 85–82.

*Weiblen, G. D. & Bush, G. L. (2002). Speciation in fig pollinators and parasites. *Molecular Ecology* **11**, 1573–1578.

Weisse, T. (2007). Distribution and diversity of aquatic protists: an evolutionary and ecological perspective. In *Protist Diversity and Geographical Distribution Topics in Biodiversity and Conservation* pp. 9–25 (eds W. Foissner and D. L. Hawksworth). Springer.

Weisse, T., Berendonk, T., Kamjunke, N., Moser, M., Schessel, U., Stadler, P. & Weithof, G. (2011). Significant habitat effects influence protist fitness: evidence for local adaptation from acidic mining lakes. *Ecosphere* **2**, 1–14.

*Whipps, C. M. & Kent, M. L. (2006). Phylogeography of the cosmopolitan marine parasite *Kudoa thyristes* (Myxozoa: Myxosporea). *The Journal of Eukaryotic Microbiology* **53**, 364–373.

Whitaker, M. R., Salzman, S., Sanders, J., Kaltenpoth, M. & Pierce, N. E. (2016). Microbial communities of lycaenid butterflies do not correlate with larval diet. *Frontiers in Microbiology* **7**, 1920.

Whitaker, R. J. (2006). Allopatric origins of microbial species. *Philosophical Transactions of the Royal Society: B Biological Sciences* **361**, 1975–1984.

Widmer, A., Lexere, C. & Cozzolino, S. (2009). Evolution of reproductive isolation in plants. *Heredity* **102**, 31–38.

Wiens, J. J. (2004). Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* **58**, 193–197.

Wiens, J. J. (2017). What explains patterns of biodiversity across the Tree of Life? *BioEssays* **39**, 1600128.

Wiens, J. J. (2021). Vast (but avoidable) underestimation of global biodiversity. *PLoS Biology* (in press).

Wiens, J. J., Lapoint, R. T., & Whiteman, N. K. (2015). Herbivory increases diversification across insect clades. *Nature Communications* **6**, 8370.

Willis, B. L., van Oppen, M. J. H., Miller, D. J., Vollmer, S. V. & Ayre, D. J. (2006). The role of hybridization in the evolution of reef corals. *Annual Review of Ecology, Evolution and Systematics* **37**, 489–517.

*Williams, S. T. (2007). Origins and diversification of Indo-West Pacific marine fauna: evolutionary history and biogeography of turban shells (Gastropoda, Turbinidae). *Biological Journal of the Linnean Society* **92**, 573–592.

*Williams, S. T. & Reid, D. G. (2004). Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* **58**, 2227–2251.

*Wilson, A. B., Glaubrecht, M. & Meyer, A. (2004). Ancient lakes as evolutionary reservoirs: evidence from the thalassoid gastropods of Lake Tanganyika. *Proceedings of the Royal Society of London B: Biological Sciences* **271**, 529–536.

*Wilson, N. G., Maschek, J. A. & Baker, B. J. (2013). A species flock driven by predation? Secondary metabolites support diversification of slugs in Antarctica. *PLoS One* **8**, 1–7.

*Winston, M. E., Kronauer, D. J. C. & Moreau, C. S. (2017). Early and dynamic colonization of Central America drives speciation in Neotropical army ants. *Molecular Ecology* **26**, 859–870.

Wollenberg, K. C., Vietes, D. R., Glaw, F. & Vences, M. (2011). Speciation in little: the role of range and body size in the diversification of Malagasy mantellid frogs. *BMC Evolutionary Biology* **11**, 217.

Wolstenholme, J. K. (2004). Temporal reproductive isolation and gametic compatibility are evolutionary mechanisms in the *Acropora humilis* species group (Cnidaria; Scleractinia). *Marine Biology* **144**, 567–582.

Wood, T. E., Takebayashis, N., Barker, M. S., Mayrose, I., Greenspoon, P. B. & Rieseberg, L. H. (2009). The frequency of polyploid speciation in vascular plants. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 13875–13879.

*Wood, T. K. (1980). Divergence in the *Enchenopa binotata* complex (Homoptera: Membracidae) effected by host plant adaptation. *Evolution* **34**, 147–160.

*Wood, T. K. & Guttman, S. I. (1982). Ecological and behavioral basis for reproductive isolation in the sympatric *Enchenopa binotata* complex (Homoptera: Membracidae). *Evolution* **36**, 233–242.

*Wood, T. K. & Guttman, S. I. (1983). *Enchenopa binotata* complex: sympatric speciation? *Science* **220**, 310–312.

*Wood, T. K. & Keese, M. C. (1990). Host-plant-induced assortative mating in *Enchenopa* treehoppers. *Evolution* **44**, 619–628.

*Wood, T. K., Tilmon, K. J., Shantz, A. B. & Harris, C. K. (1999). The role of host-plant fidelity in initiating insect race formation. *Evolutionary Ecology Research* **1**, 317–323.

*Wörheide, G., Degnan, B. M., Hooper, J. N. A. & Reitner, J. (2000). Phylogeography and taxonomy of the Indo-Pacific reef cave dwelling coralline demosponge *Astrosclera willeyana*—new data from nuclear internal transcribed spacer sequences. In *Proceedings of the 9th International Coral Reef Symposium* (ed. K. Moosa), pp. 339–346; International Coral Reef Symposium (ICRS).

Wylezich, C., Karpov, S. A., Mylknikov, A. P., Anderson, R. & Jurgens, K. (2012). Ecologically relevant choanoflagellates collected from hypoxic water masses of the Baltic Sea have untypical mitochondrial cristae. *BMC Microbiology* **12**, 271.

*Xue, H.-J., Li, W.-Z. & Yang, X.-K. (2014). Assortative mating between two sympatric closely-related specialists: inferred from molecular phylogenetic analysis and behavioral data. *Scientific Reports* **4**, 5436.

*Xue, H.-J., Li, W.-Z., Nie, R.-E. & Yang, X.-K. (2011). Recent speciation in three closely related sympatric specialists: inferences using multi-locus sequence, post-mating isolation and endosymbiont data. *PLoS One* **6**, 1–9.

*Yasuda, N., Taquet, C., Nagai, S., Fortes, M., Fan, T., Phongsuwan, N. & Nadaoka, K. (2014). Genetic structure and cryptic speciation in the threatened reef-building coral *Heliopora coerulea* along Kuroshio Current. *Bulletin of Marine Science* **90**, 233–255.

*Yawson, A. E., Weetman, D., Wilson, M. D. & Donnelly, M. J. (2007). Ecological zones rather than molecular forms predict genetic differentiation in the malaria vector *Anopheles gambiae s.s.* in Ghana. *Genetics* **175**, 751–761.

Yuan, Y. W., Sagawa, J. M., Young, R. C., Christensen, B. J. & Bradshaw, H. D. (2013). Genetic dissection of a major anthocyanin QTL contributing to pollinator-mediated reproductive isolation between sister species of *Mimulus*. *Genetics* **194**, 255–263.

*Yukilevich, R. (2012). Asymmetrical patterns of speciation uniquely support reinforcement in *Drosophila*. *Evolution* **66**, 1430–1446.

*Yukilevich, R. (2013). Tropics accelerate the evolution of hybrid male sterility in *Drosophila*. *Evolution* **67**, 1805–1814.

Yukilevich, R. (2014). The rate test of speciation: estimating the likelihood of non-allopatric speciation from reproductive isolation rates in *Drosophila*. *Evolution* **68**, 1150–1162.

*Yukilevich, R., Maroja, L. S., Nguyen, K., Hussain, S. & Kumaran, P. (2018). Rapid sexual and genomic isolation in sympatric *Drosophila* without reproductive character displacement. *Ecology and Evolution* **8**, 2852–2867.

Yun, J.-H., Roh, S. W., Whon, T. W., Jung, M.-J., Kim, M.-S., Park, D.-S., Yoon, C., Nam, Y.-D., Kim, Y.-J., Choi, J.-H., Kim, J.-Y., Shin, N.-R., Kim, S.-H., Lee, W.-J. & Bae, J.-W. (2014). Insect gut bacterial diversity determined by environmental habitat, diet, developmental stage, and phylogeny of host. *Applied and Environmental Microbiology* **80**, 5254–5264.

Zeh, D. W. & Zeh, J. A. (2000). Reproductive mode and speciation: the viviparity-driven conflict hypothesis. *BioEssays* **22**, 938–946.

*Zervakis, G. I., Moncalvo, J. M. & Vilgalys, R. (2004). Molecular phylogeny, biogeography and speciation of the mushroom species *Pleurotus cystidiosus* and allied taxa. *Microbiology* **150**, 715–726.

*Zhang, B., Segraves, K. A., Xue, H.-J., Nie, R.-E., Li, W.-Z. & Yang, X.-K. (2015). Adaptation to different host plant ages facilitates insect divergence without a host shift. *Proceedings of the Royal Society of London B: Biological Sciences* **282**, 282, 20151649.

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.