



REVIEW ARTICLE

Reproductive isolation and the causes of speciation rate variation in nature

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Rates of species formation vary widely across the tree of life and contribute to many of the most striking large-scale patterns in biological diversity. For the past few decades, most research on speciation has focused on the evolution of barriers to gene flow between populations. The present review discusses the relationship between these barriers, collectively known as ‘reproductive isolation’, and the rate at which speciation occurs. Although reproductive isolation plays a key role in the maintenance of biological diversity, there is little evidence to suggest that any forms of reproductive isolation serve as rate-limiting controls on speciation rates as measured over macroevolutionary timescales. Identifying rate-limiting steps of the speciation process is critical for understanding why we observe the numbers of species that we do and also for explaining why some groups of organisms have more species than others. More generally, if reproductive isolation is not the rate-limiting control on speciation rates, then factors other than reproductive isolation must be involved in speciation and our definition of speciation should be expanded to incorporate these additional processes. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 13–25.

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INTRODUCTION

At any given location on Earth, biological diversity is packaged into more-or-less discrete units that we typically refer to as ‘species’. This fact has been evident to naturalists and philosophers for many centuries and is reflected by the ease with which you can use a field guide to identify the birds and trees in your backyard. Science has settled the matter of whether these distinct groups (species, hereafter) exist in a general sense (Mayr, 1992; Rieseberg, Wood & Baack, 2006), even if the boundaries of any particular species in space and time may be unclear. Even Darwin, who was famously skeptical about the reality of species as a special category, felt that they represented ‘tolerably well-defined objects’ (Darwin, 1859).

In the first half of the 20th Century, ideas about species and speciation underwent a revolution that shapes much of the prevailing paradigm for understanding the origins of biological diversity. This revolution involved a new conceptualization of species, one where species were defined by the processes that kept them apart. These processes, collectively termed ‘reproductive isolation’, formed the cornerstone of the new ‘biological species concept’. The biological species concept (BSC) was popularized by Ernst Mayr (Mayr, 1942, 1963) and generally defines species as ‘groups of interbreeding natural populations that are reproductively isolated from other such groups’ (Mayr, 1970).

Reproductive isolation can take many forms. It may involve the presence of distinctive morphological, behavioural or other signals that are involved in mate recognition. It may involve ecological factors that affect the fitness of hybrid offspring in nature. For example, hybrid genotypes may have lower survivorship than pure genotypes of either parental

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form. Reproductive isolation may involve genetic incompatibilities between species that result in the sterility or inviability of hybrid offspring. There are many potential barriers to gene flow, and they have been catalogued at length in recent treatments of speciation (Coyne & Orr, 2004; Price, 2008; Sobel *et al.*, 2010; Nosil, 2012).

The study of speciation has largely been the study of the factors that generate and maintain reproductive isolation (Coyne & Orr, 2004; Wu & Ting, 2004; Mahehwarri & Barbash, 2011; Nosil, 2012). In a recent introductory textbook on evolutionary biology (Futuyma, 2009), speciation is defined as the ‘evolution of reproductive isolation within an ancestral species, resulting in two or more descendant species’. This view clearly dominates across most of evolutionary biology. In their seminal book on speciation, Coyne & Orr (2004: 39) observed that ‘virtually every recent paper on the origin of species, theoretical or experimental, deals with the origin of isolating barriers’. This fact is unsurprising because reproductive isolation must be the principal concern of a speciation paradigm that defines the process in terms of reproductive isolation itself.

In this review, I argue that a near-exclusive focus on reproductive isolation in speciation research has hindered our ability to explain large-scale diversity patterns. It is increasingly evident that the rate at which speciation occurs varies widely across the tree of life (Smith *et al.*, 2011; Jetz *et al.*, 2012; Beaulieu & Donoghue, 2013; Near *et al.*, 2013; Rabosky *et al.*, 2013), and we know very little about the factors that determine these rates. Many of the most striking large-scale patterns in biological diversity are macroevolutionary in nature and can only be answered, at least in part, by understanding the determinants of the rate at which speciation occurs. Why are there so many species of flowering plants? Why are there 60 000 species of living vertebrates and not 6000 or 600 000? Why are lungfishes and coelacanths and ginkgoes so depauperate in species diversity? Why are there so many species in the tropics? Of course, diversity is a function of both speciation and extinction, and it is the relative balance of these processes that determines the dynamics of species richness in time. Although some of the patterns described above may reflect variation in extinction rates (rather than speciation *per se*), many studies that have explicitly modelled the contribution of speciation rate variation to large scale diversity patterns have found a compelling signal of differential speciation on diversity patterns (Rabosky *et al.*, 2013; Belmaker & Jetz, 2015; Rabosky, Title & Huang, 2015).

All of the questions outlined above (and many more) are ultimately questions about which factor or factors are ‘rate-limiting controls’ on speciation and/

or extinction dynamics as measured at macroevolutionary scales. More generally, we cannot assume that the causes of population splitting observed over short timescales can be extrapolated to the dynamics of species that play out over vastly longer geological timescales without rigorous tests to support this assumption. I advocate a more inclusive view of speciation that accounts for alternative processes, largely neglected in contemporary speciation research, which may provide the rate-limiting controls on the generation of biological diversity.

TAXONOMIC SPECIATION RATES

Most research on the origin of species has focused on reproductive isolation, although a parallel research programme on speciation rates has proceeded without interpreting patterns through the framework of reproductive isolation. This approach has its roots in the palaeobiological revolution of the 1970s, in which quantitative models for species formation and extinction were developed to study the appearances and disappearances of individual taxa from the fossil record (Raup *et al.*, 1973; Stanley, 1975; Sepkoski, 1978; Raup, 1985). The statistical tools developed for studying speciation in the fossil record (Raup, 1985) have been applied to time-calibrated phylogenetic trees that contain information on living species only (Nee, May & Harvey, 1994; Rabosky & Lovette, 2008; Morlon, Potts & Plotkin, 2010; Etienne & Haegeman, 2012; Pyron & Burbrink, 2013; Stadler, 2013; Moen & Morlon, 2014). These methods have been used to quantify speciation rates in a wide range of taxa, spurred by the rapid increase in the availability of time-calibrated phylogenetic trees based on DNA sequence data.

From a macroevolutionary perspective, the rate of speciation is a statistical description of the per-species rate at which new taxonomic diversity arises. These rates are referred to here as ‘taxonomic speciation rates’ to reflect the fact that they are based on species units as recognized by taxonomic practice. To be clear, the reference is to rates of new species origination (i.e. the rate of appearance of new species, as defined taxonomically) and not net rates of lineage diversification. Net rates of lineage diversification reflect the balance of species origination and extinction and determine the dynamics of species richness through time; this is not the same as the rate at which diversity arises, which is the focus of the present review. As discussed below, these taxonomic speciation rates are not necessarily the same as ‘biological speciation rates’, defined by Coyne & Orr (2004) as the rate at which reproductively isolated lineages arise. Palaeontological studies demonstrated

variation in evolutionary rates among major groups of organisms (Stanley, 1979; Jablonski, 1986; Sepkoski, 1998), although phylogenetic diversification studies have provided a much higher level of resolution into the dynamics of speciation (but not extinction; Ezard *et al.*, 2011). One of the most important results emerging from this research is the extent to which taxonomic speciation rates vary, even between closely-related groups of organisms. Figure 1 shows a pattern of speciation rate variation across a phylogeny of living birds (Jetz *et al.*, 2012), as inferred using a recently-developed method for quantifying speciation rate heterogeneity (Rabosky, 2014). Across all birds, speciation rates measured over macroevolutionary timescales vary by approximately 3000% (Rabosky *et al.*, 2015).

INTERPRETATION OF ‘SPECIATION RATE’ DEPENDS ON THE MEANING OF SPECIES

Species delimited by the strict application of the biological species concept do not necessarily correspond to the set of species defined by taxonomic practice. Despite the view among many population geneticists that the BSC is mainstream in modern evolutionary biology, taxonomic practice largely ignores the BSC and species are generally defined on the basis of phenotypic distinctiveness (Mallet, 2007), occasionally with supporting evidence from molecular phylogenies or population genetics. Coalescent-based species delimitation using population genetic data (Pons *et al.*, 2006; Yang & Rannala, 2010) represents a trend towards greater practical application of BSC-like species concepts to taxonomy (Fujita *et al.*, 2012), although the use of these models is still restricted to a small fraction of annual taxonomic volume. Despite the use of sophisticated species delimitation approaches in general phylogenetics journals with a broad readership (e.g. *Systematic Biology*; *Molecular Phylogenetics and Evolution*), the trade journals of taxonomy (e.g. *Zootaxa*), where the vast majority of new species are described, overwhelmingly utilize morphological distinctiveness as the primary criterion for species status.

In some groups, there is evidence that reproductively isolated populations of very recent origin are rarely recognized as distinct (taxonomic) species. For example, autopolyploid lineages in plants are generally not recognized as distinct from the progenitor species, even when such recognition is potentially warranted under the BSC (Soltis *et al.*, 2007). Hundreds, perhaps thousands, of fish lineages in postglacial lakes across North America, Eurasia, and Iceland have diverged into phenotypically and ecologically distinctive forms (Skulason, Noakes &

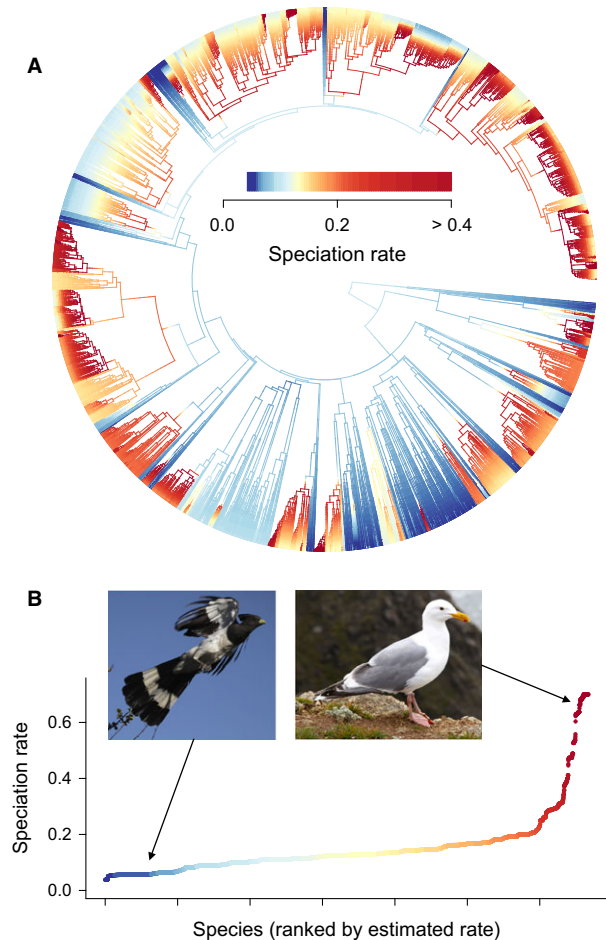


Figure 1. A, per-lineage rates of speciation across a time-calibrated phylogenetic tree of 6670 species of extant birds (67% of the total diversity) as inferred using a statistical model that simultaneously estimates the magnitude of rate variation through time and across lineages. Colours correspond to the instantaneous rate of speciation at each point in the tree. The fastest 5% of rates exceed 0.4 species Myr⁻¹ (dark red). Analysis of evolutionary rates explicitly accounts for extinction, although only speciation rates are shown. B, estimated present-day speciation rates for all 6670 species; these are simply the best estimate of the instantaneous rate of speciation for each tip in the phylogeny. Inset images depict representative birds with fast (western gull, *Larus occidentalis*) and slow (go-away-bird, *Corythaixoides leucogaster*) rates of speciation. The phylogenetic dataset is from Jetz *et al.* (2012) and speciation rate analysis is described in Rabosky & Matute (2013).

Snorrason, 1989; Bernatchez, Chouinard & Lu, 1999; McKinnon & Rundle, 2002; Hudson *et al.*, 2005), yet these forms are very rarely afforded full species status by taxonomists. Many of these divergent within-lake fish lineages are unlikely to predate the last glacial cycle (approximately 30 000 years BP).

Including these forms as full species in macroevolutionary rate analyses would lead to a substantially different interpretation of speciation rate (Fig. 2).

The relationship between species under the BSC and taxonomic practice is complex and will not be reviewed here. However, it is important to recognize that speciation rates as typically inferred from phylogenetic and palaeontological data need not correspond to those that we would estimate if we were to apply the BSC consistently across all lineages within the same group of organisms. The ‘biological speciation rate’ as described by Coyne & Orr (2004) is, in practice, a taxonomic speciation rate, and it may be distinct from the rate at which reproductively isolated lineages arise. Despite the inherent fuzziness of ‘species’ as used in macroevolutionary studies, they are all that we have to work with until units at the tips of the tree of life are delimited using equivalent criteria. Given the difficulty in identifying a single species concept that works for all groups of organisms (Van Valen, 1976; Harrison, 1998; Mallet, 2007; de Queiroz, 2007), it is unlikely that we will ever achieve such equivalence. My view is that, given the general reluctance to ascribe full species status to very recently diverged forms, the ‘taxonomic species concept’ that underlies evolutionary rate estimates is biased towards the recognition of deeper lineages and generally neglects recent divergences that might be labeled ‘incipient

species’, ‘isolates’ (Mayr, 1963), ‘neospecies’ (Levin, 2000) or ‘within-species lineages’ (Dynesius & Jansson, 2014). As such, ‘speciation rates’ as estimated from established taxonomies will generally describe lineage dynamics at a phylogenetic scale that ignores the rate at which incipient species are generated.

WHAT CONTROLS THE RATE OF SPECIATION?

Reproductive isolation is clearly an important component of the speciation process and is critical for the maintenance of diversity. In the absence of reproduc-

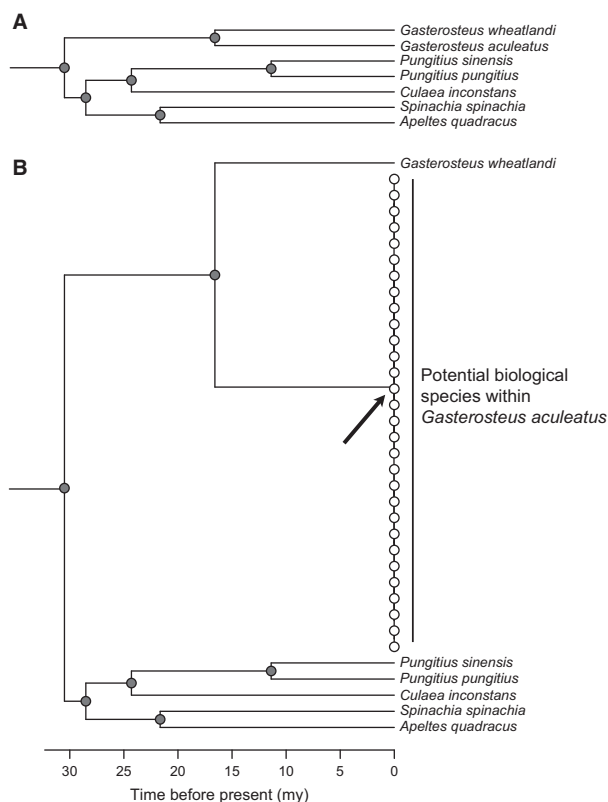


Figure 2. Alternative species taxonomies can lead to radically different perspectives on species and speciation. A, time-calibrated phylogeny for stickleback fishes (*Gasterosteidae*) from Rabosky *et al.* (2013). Divergence times are broadly congruent with the known fossil history for the genus (Bell, Stewart & Park, 2009). B, hypothetical shape of the stickleback phylogeny if some of the numerous intraspecific morphological variants (open circles) within the threespine stickleback (*Gasterosteus aculeatus*) are elevated to full species status. Many freshwater stickleback populations are morphologically distinct from the marine ancestral form and potentially warrant recognition as distinct biological species (Moodie & Reimchen, 1976; Mcphail, 1994; Bell, 1995; Nelson, 2006; Reimchen *et al.*, 2013); there are potentially dozens or hundreds of such forms. Bell (1995) suggests that, given the extent of morphological parallelism among divergent forms, ‘... it is neither practical nor useful to describe the biological species within the *G. aculeatus* complex as separate taxonomic species’. However, given that many such forms could be recognized as distinct taxonomic species, it is worth considering how their recognition would change our interpretation of speciation rates. Previous studies on speciation rates across fishes (Near *et al.*, 2013; Rabosky *et al.*, 2013) include only information from deep nodes (dark circles). However, recent divergences, almost all of which are no older than the most recent glacial maximum (arrow), are ignored by this approach. For the phylogeny in (A), the maximum likelihood estimate of the speciation rate under a constant-rate birth-death model (Nee *et al.*, 1994) is 0.055 lineages Myr^{-1} . For the phylogeny in (B), which assumes the presence of 30 biological species in ‘*Gasterosteus aculeatus*’, all of which have diverged within the past 30 000 years, we infer a speciation rate of 65.4 lineages Myr^{-1} . The number of recently-diverged species spliced into the phylogeny shown in (B) is arbitrary, although it illustrates the profound effects that taxonomic decisions can have on inferences about speciation rate. Understanding the relationship between speciation as studied at population genetic scales (open circles) and macroevolutionary scales (dark circles) is one of the central challenges for the future of speciation research.

tive isolation, interbreeding between (sexual) species should result in the collapse of taxonomic diversity. This phenomenon is clearly not what we observe: many species are able to coexist in the same location at the same time as maintaining their distinctiveness. However, other factors can influence taxonomic speciation rates yet are distinct from reproductive isolation (Allmon, 1992; Levin, 2000; Rosenblum *et al.*, 2012). Ernst Mayr, an architect of the biological species concept, provided one of the clearest statements of major factors that determine speciation rates. In *Animal Species and Evolution* (1963), Mayr notes that the rate of speciation depends on:

‘... (1) the frequency of barriers, that is, of factors producing geographical isolates, (2) the rates at which geographical isolates become genetically transformed and more specifically at which they acquire isolating mechanisms, and (3) the degree of ecological diversity offering vacant ecological niches to newly arising species’ (Mayr, 1963: 575).

Among these three categories, only item (2) would traditionally be associated with reproductive isolation. Mayr explains that item (3) – ecological niche availability – is important for successful speciation, because the presence of a vacant niche enables incipient species (‘isolates’) to persist in time. As Mayr stated (Mayr, 1963: 554): ‘What does it matter if 98 or 99 percent among 100 founder populations or other isolates fall by the wayside? All is well and evolutionary progress assured as long as one of them once in awhile discovers a new niche’. There is an irony to the set of controls listed here because Mayr (along with Theodosius Dobzhansky) is one of the scientists most widely credited for focusing our collective attention on reproductive isolation as the defining feature of speciation (Coyne & Orr, 2004).

More recently, Allmon (1992) and Dynesius & Jansson (2014) reformulated Mayr’s three controls on speciation, noting that, in some cases, several of these components may interact synergistically. Table 1 provides an overview of the general types of processes that can influence taxonomic speciation rates.

As discussed above, diversification rate is the difference between per-taxon speciation and extinction rates and determines the expected diversity of a clade through time. The semantics of extinction cannot be ignored because one of the major controls on speciation identified (Mayr, 1963; Allmon, 1992; Stanley, 2008; Rosenblum *et al.*, 2012) involves the persistence (e.g. ‘non-extinction’) of isolated populations or incipient species through time (Table 1). The boundary between speciation and extinction may be much blurrier than we typically acknowledge. At the macroevolutionary scale, ‘extinction’ is applied to taxa that are diagnosable in the fossil record and that have had a history of existence as independent evolutionary lineages.

A failure of incipient forms to persist is conceptually distinct from extinction as typically understood because it involves populations that have had only the briefest existence as independent lineages. The persistence control can apply to lineages that are geographically isolated but that show no reproductive isolation and no diagnostic phenotypic traits relative to a parental population. It is inappropriate to assume equivalence between extinction at the macroevolutionary scale (e.g. the loss of a species) and extinction of potentially localized populations, which might simply represent demographic loss within a single undifferentiated species. Moreover, the failure of recently-isolated populations to persist, whether they are reproductively isolated or not, is largely invisible in the fossil record (Rabosky, 2013).

Table 1. Controls on speciation rates as measured at macroevolutionary scales: examples are speculative but show characteristics suggesting the action of the focal control

Control	Description	Possible examples
Rate of splitting	The rate at which a single population splits into two populations	High rates of long-distance dispersal in <i>Zosterops</i> birds (‘white-eyes’) leads to the establishment of new populations on remote islands and to rapid speciation rates for the clade as a whole (Moyle <i>et al.</i> , 2009)
Reproductive isolation	Evolution of biological traits that reduce gene flow between populations	Reproductive isolation, mediated by mating preferences and male colour phenotypes, evolves rapidly between populations of Lake Victoria cichlid fishes (Seehausen <i>et al.</i> , 2008). This group is known to have extremely rapid rates of speciation (Johnson <i>et al.</i> , 1996)
Population persistence	Incipient species avoid demographic extinction	Similarity to parental forms may limit persistence of recently-formed polyploid plant species (Levin, 2000; Mayrose <i>et al.</i> , 2011; Arrigo & Barker, 2012)

As such, there is (in general) no observable extinction associated with the failure of incipient forms to persist.

Our general binary distinction between speciation and extinction thus leads to terminological confusion when discussing these processes. From the macroevolutionary perspective adopted in the present review, I agree with Mayr's view that 'persistence of incipient species' is a part of the concept of speciation and separate from the processes by which established lineages become extinct. This distinction follows naturally from a conceptualization of species origination that can be measured over palaeontological or phylogenetic scales. Moreover, treating persistence as part of speciation is warranted on strictly pragmatic grounds if we are to continue studying speciation rates using time-calibrated phylogenies of extant taxa and the fossil record. Barring a radical change in taxonomic practice, speciation rates as measured at a macroevolutionary scale (and as published in hundreds of recent journal articles) are an outcome of the three controls discussed above. Hence, even formal models that can distinguish between speciation and extinction rates on phylogenetic trees (Maddison, Midford & Otto, 2007; FitzJohn, Maddison & Otto, 2009; Goldberg, Lancaster & Ree, 2011) are unable to separate the effects of lineage persistence from other factors that influence speciation rate (but, for a useful analytical approach to this problem, see Etienne, Morlon & Lambert, 2014). However, ultimately, it will be most fruitful if we move beyond a dichotomous view of speciation and extinction as the fundamental processes of lineage diversification (as many researchers cited in the present review have already done).

Successful speciation thus entails the splitting of populations, the evolution of biologically-based barriers to gene flow (reproductive isolation), and the persistence of incipient species. All of these general factors might be involved in the speciation process, although it is the rate-limiting factor alone, which could be any of the three, that determines the taxonomic speciation rate. This rate, together with the rate at which established lineages go extinct, is the most important with respect to explaining why the 'quantity' of biological diversity is what we observe it to be. These factors are not mutually exclusive. For example, divergent natural selection that favours multiple phenotypes within a species can simultaneously promote population splitting and reproductive isolation, as in models where speciation occurs in the presence of substantial gene flow (Gagnaire *et al.*, 2013; Martin *et al.*, 2013). Anecdotally, it is clear that reproductive isolation can evolve rapidly in some taxa that have slow rates of speciation as

measured at macroevolutionary timescales (Rabosky, 2013). Stickleback fishes can evolve reproductive isolation quite rapidly and have formed morphologically distinctive populations or even pairs of incipient species in many postglacial lakes (Schluter, 1996; Rundle *et al.*, 2000; Reimchen, Bergstrom & Nosil, 2013). These differences have potentially evolved subsequent to the Last Glacial Maximum (< 30 000 years BP). However, incipient stickleback forms only rarely become taxonomically distinct species because they fail to persist through deep time (McKinnon & Rundle, 2002). McPhail (1994) discussed the paradox between the low species richness of stickleback fishes in general (Fig. 2) and their propensity for rapid speciation in the present day: '... most divergent [stickleback] populations and biological species that evolve under these conditions are doomed either to genetic swamping or to extinction. They flourish briefly and then disappear without appreciable impact on the evolutionary trajectory of the main body of the species' (McPhail, 1994: 437). Hence, reproductive isolation does not appear to be a rate-limiting control on stickleback speciation rates as measured over macroevolutionary timescales.

The situation in nature is rather more complex than that suggested by the outline above because reproductive isolation is often incomplete and, at least in some taxa, has been shown to break down in ecological time (Seehausen, van Alphen & Witte, 1997; Nosil, Harmon & Seehausen, 2009). For example, in North America's Great Lakes, an endemic species flock of *Coregonus* whitefishes appears to have undergone 'speciation in reverse' in historical times. Most forms appear to have disappeared as a result of hybridization (Todd & Stedman, 1989), and similar merging of incipient or recently diverged forms has occurred in stickleback fishes (Gow, Peichel & Taylor, 2006; Taylor *et al.*, 2006) and Lake Victoria cichlids (Seehausen *et al.*, 1997). Darwin's finches are another example of a group where reproductive isolation between morphological forms appears to lack temporal stability (Grant & Grant, 1997), leading to widespread genetic homogenization among morphological forms inhabiting the same island (Farrington *et al.*, 2014; McKay & Zink, 2015). It would be premature, however, to conclude that the limiting step on taxonomic speciation rates in these and other taxa is a function of the robustness of reproductive isolation and not of other potential controls.

Many studies have addressed the relationships between specific organismal traits and speciation rates on phylogenetic trees. This literature is not reviewed here, in part because the mechanisms by which traits influence speciation are rarely known or directly tested. For example, an association between

a key ecological trait and speciation rate could arise if the trait accelerates the evolution of reproductive isolation in lineages where it is present. However, it is also possible that the trait influences the speciation rate through its effects on population persistence or establishment. Thus, the connection between traits and speciation generally relies on assumptions about the relevance of the trait for the controls described above. An alternative approach that more directly connects specific components of reproductive isolation to taxonomic speciation rates is discussed below. Nonetheless, a number of researchers have considered the effects of dispersal and geographical range dynamics for speciation rate (Sol, Stirling & Lefebvre, 2005; Weeks & Claramunt, 2014); these processes presumably influence speciation not through their effects on reproductive isolation, but through the establishment of new populations (Price, 2010) and/or by facilitating population persistence (Harnik, Simpson & Payne, 2012). Price *et al.* (2014) suggested that speciation rates in Himalayan passerine birds were influenced more by ecological controls on range expansions than by the build up of reproductive isolation. An interesting twist on the speciation controls listed above is that incomplete reproductive isolation may itself limit range expansion (Weir & Price, 2011), thus indirectly facilitating population persistence (through larger geographical range), as well as the establishment of new populations for subsequent speciation. This idea remains to be tested but would support the possibility that reproductive isolation and other controls may interact to jointly influence the rate of speciation.

It is generally accepted that some forms of reproductive isolation might have little relevance to the speciation process. For example, intrinsic postzygotic isolation (i.e. genetic incompatibilities between species that cause hybrid dysfunction) might arise long after successful speciation has occurred (Grant & Grant, 1997; Coyne & Orr, 2004; Bolnick & Near, 2005; Wiens, Engstrom & Chippindale, 2006), implying that these forms of reproductive isolation contribute little to the speciation process. However, there is no evidence available indicating that any forms of reproductive isolation serve as rate-limiting controls on taxonomic speciation rates. To be clear, there is little evidence to suggest that any other controls (Table 1) are generally more important than reproductive isolation at this scale, although few studies have yet assessed the relative contributions of these factors to variation in speciation rate. Identifying these controls and clarifying their genetic, demographic, and ecological mechanisms is one of the greatest challenges for evolutionary biology in the coming years.

TESTING THE ROLE OF REPRODUCTIVE ISOLATION IN SPECIATION DYNAMICS

Because reproductive isolation can be quantified, it is possible to directly test whether it is a rate-limiting control on taxonomic speciation rates (Rabosky & Matute, 2013). All else being equal, lineages that evolve reproductive isolation more quickly should be characterized by faster rates of speciation. As a thought experiment, consider two distinct species, X and Y , such that X belongs to a clade of organisms that can evolve reproductive isolation rapidly, and Y belongs to a clade where reproductive isolation evolves slowly. Suppose that a geological event splits both species X and Y into two populations: X_1 and X_2 , and Y_1 and Y_2 . After an equivalent amount of time has elapsed, populations X_1 and X_2 would show greater reproductive isolation than populations Y_1 and Y_2 . If the rate at which reproductive isolation evolves is the rate-limiting control on speciation rates, then the lineage to which species X belongs should, over long timescales, speciate more rapidly than the lineage of Y . If another factor is the rate-limiting control on speciation rates, then the realized rate of speciation will be independent of the rate at which reproductive isolation evolves.

This logic forms the basis of a statistical test for the contribution of any form of reproductive isolation to macroevolutionary speciation rates. One can quantify the rate at which particular components of reproductive isolation evolve in different clades or lineages (Fig. 3) and test whether variation in the rate of evolution of reproductive isolation predicts speciation rates. Possible relationships between these quantities are shown in Figure 4. The key advantage of this approach is that it avoids assumptions about the presumed effects of particular organismal traits on the evolution of reproductive isolation (Coyne & Orr, 2004) and estimates parameters of the process directly. This test has been applied to birds and to drosophilid flies aiming to test whether the rate at which lineages acquire postzygotic genetic incompatibilities (e.g. alleles that cause interspecies hybrids to be sterile or inviable) is associated with speciation rates. Although individual clades of both birds and flies varied with respect to the rate at which they evolved at least one component of reproductive isolation, this variation was unrelated to taxonomic speciation rates (Rabosky & Matute, 2013). However, the results reported by Rabosky & Matute (2013) should be interpreted with circumspection, given uncertainties in quantifying speciation rate variation and the rate at which reproductive isolation evolves. For example, the biology of intrinsic reproductive isolation in drosophilid flies has been studied by dozens of researchers over much of the past century,

generating perhaps the highest-resolution dataset on reproductive isolation for any group of organisms (Yukilevich, 2012). However, our understanding of taxonomic speciation rates in the drosophilidae is poor: indeed, it is possible that hundreds or thousands of distinct drosophilid taxa remain to be described (Markow & O'Grady, 2006). Such taxonomic inadequacy has implications for the speciation rates used by Rabosky & Matute (2013). Similarly, our analyses of avian postzygotic isolation were largely based on a single compilation of avian hybrids (Gray, 1958) and we had no direct information on pre-mating isolation for birds.

Coyne & Orr (2004) distinguished between two temporal aspects of the speciation process: the 'biological speciation interval' (BSI), or the waiting time between the origin of new reproductively isolated lineages, and the 'transition time for biological speciation', or the amount of time required for strong

reproductive isolation to evolve once the evolution of isolation has begun. The biological speciation rate is simply the inverse of the biological speciation interval ($1/BSI$). Coyne & Orr (2004) suggested that there is little reason to expect equivalence between transition times and biological speciation intervals. However, the rate at which reproductive isolation evolves can still be the rate-limiting step on speciation rates even if transition times are much shorter (or longer) than BSIs. For example, the occurrence of partial intrinsic postzygotic isolation between populations might trigger reinforcement, such that complete prezygotic isolation evolves rapidly in response to maladaptive hybridization (Servedio & Noor, 2003; Matute, 2010). As such, the rate-limiting step on taxonomic speciation rates can still be the rate at which the initial postzygotic isolation arises, even if it is the subsequent evolution of pre-mating isolation that ultimately drives speciation to completion. This process would potentially be testable by developing more sophisticated modelling frameworks that enable researchers to distinguish between lineage-specific differences in the rate at which any measurable reproductive isolation arises (e.g. duration of the lag phase; Mendelson, Inouye & Rausher, 2004) from the rate at which strong reproductive isolation arises.

A desirable feature of the approach illustrated in Figure 4 is that it provides a fairly direct test of the contribution of reproductive isolation to taxonomic speciation rate. As such, the approach can be contrasted with phylogenetic comparative methods for identifying correlations between specific organismal

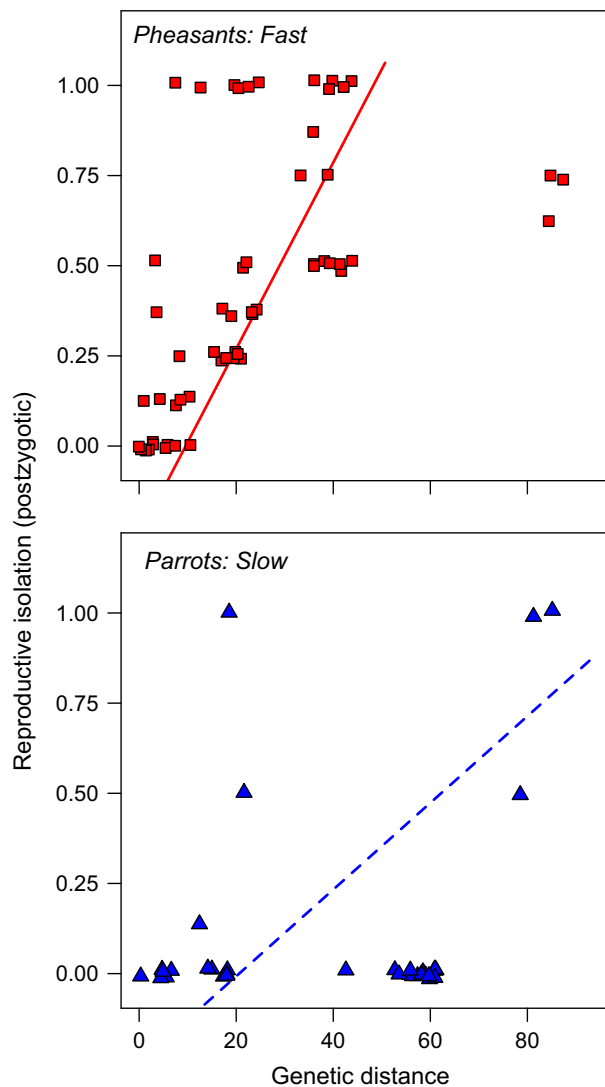


Figure 3. Pairwise postzygotic isolation from interspecific crosses of birds as a function of the pairwise genetic distance between them. Results are shown for two major clades (pheasants, Phasianidae; parrots, Psittacidae). For a given level of genetic divergence, pheasants show greater levels of postzygotic isolation than the parrots, indicating that this sort of reproductive isolation accumulates more quickly in pheasants than in parrots. If intrinsic postzygotic isolation (hybrid inviability and sterility) is the dominant control on speciation rates, pheasants should have faster rates of speciation than parrots. Note that relationships are bounded at 0 (all hybrid offspring fully viable and fertile) and 1 (no offspring produced, or all offspring sterile). Lines show fitted linear relationships between reproductive isolation and genetic distance for each clade. Data are from Price & Bouvier (2002) and Gray (1958); analyses are from Rabosky and Matute (2013). For this pair of clades, speciation rates are faster in the clade with faster rates of evolution of reproductive isolation (pheasants: speciation = $0.26 \text{ lineages Myr}^{-1}$; parrots: speciation = $0.22 \text{ lineages Myr}^{-1}$). However, across all birds, these quantities appear to be unrelated.

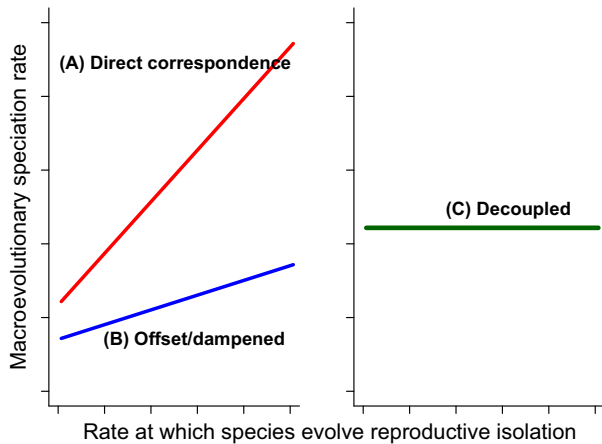


Figure 4. Some possible relationships between the rate at which lineages evolve reproductive isolation and their rate of speciation. A, direct correspondence, where the evolution of reproductive evolution shows a one-to-one relationship with the macroevolutionary rate of speciation. In this scenario, the evolution of reproductive isolation is the exclusive determinant of macroevolutionary speciation dynamics. B, offset/dampened relationship, where the rate of evolution of reproductive isolation is the dominant control on speciation rates, although speciation rates are lower than predicted by the rate of evolution of reproductive isolation alone. This relationship implies that many populations evolving reproductive isolation fail to persist through deep time. C, decoupled, such that reproductive isolation shows no predictive relationship with macroevolutionary speciation rates. This scenario suggests that reproductive isolation is not the rate-limiting control on the rate of speciation. Adapted from Rabosky (2013).

traits and diversification rates. Numerous studies have found at least some association between traits and diversification rates (Coyne & Orr, 2004; Jablonski, 2008; Ng & Smith, 2014). Such associations can arise if the traits under consideration increase the rate at which reproductive isolation evolves (Panhuis *et al.*, 2001; Coyne & Orr, 2004), to which we might add: ‘provided that the rate of evolution of reproductive isolation is the rate limiting step on taxonomic speciation rates’. However, demonstration that a particular trait is correlated with taxonomic speciation rate does not necessarily imply that the underlying mechanism involves the effects of the trait on reproductive isolation, even if we assume that the trait influences reproductive isolation. Because of the complex ways in which traits can influence metapopulation dynamics (Levin, 2000), we should be cautious in assuming that any particular traits (e.g. sexual dichromatism in animals, floral characteristics, etc.) influence species richness through their effects on reproductive isolation.

It is also important to recognize the limitations of the approach illustrated in Figure 4. The lack of a relationship between a particular control (e.g. intrinsic postzygotic reproductive isolation) and speciation rates should not be interpreted as evidence that the control is irrelevant to speciation. It simply means that the control does not determine the rate at which speciation occurs; the control may nonetheless be an integral part of the speciation process. Furthermore, observing that one component of reproductive isolation fails to predict speciation rates provides no information about the importance of other forms of reproductive isolation for speciation rates. Finally, the quality of the available phylogenetic, taxonomic, and reproductive isolation data limit the use of this framework in practice.

Other conceptual tools may provide insight into the role of splitting and persistence controls on speciation rates. The protracted speciation model (Etienne & Rosindell, 2012) is an important theoretical framework for understanding how the origination, extinction, and persistence of incipient species influence the shapes of phylogenetic trees. Recently, Etienne *et al.* (2014) developed a form of the protracted speciation model that could be fitted to phylogenetic datasets, potentially enabling researchers to estimate parameters associated with both the rate of incipient species formation and the time required for successful speciation. Conceivably, extensions of this general framework may be developed into a formal test of the relative importance of these and other controls on taxonomic speciation rates.

CONCLUSIONS

I suggest that any general theory of speciation that purports to explain large-scale patterns of biological diversity must be able to explain taxonomic speciation rates as measured using phylogenetic or palaeontological data. The present review has outlined a general framework that can be used to test whether various components of reproductive isolation serve as rate-limiting steps on the generation of biological diversity. Although I have summarized some classic and recent work on speciation rate controls (Mayr, 1963; Allmon, 1992; Rosenblum *et al.*, 2012; Dynesius & Jansson, 2014), my focus in this review has been on the relationship between reproductive isolation and taxonomic speciation rates.

A number of complex issues remain to be resolved, such as the relationship between taxonomic speciation rates and biological speciation rates. Many researchers have previously noted the consequences of species delimitation for the study of speciation (Harrison, 1998; Wiens, 2004) and I believe that

progress towards understanding speciation ultimately depends on understanding the meaning of the taxonomic units on which we base our speciation rate estimates. Concerns about the meaning of species may be even more acute for the fossil record because fossil species typically represent stratigraphically distinct morphotypes (Allmon, 2013). With the possible exception of large vertebrates (Roth, 1992), the connection between these forms and present-day (neontological) species remains poorly known.

During the past few decades, we have learned a great deal about the processes that maintain the persistence and distinctiveness of species in sympatry. We understand much about the genetic basis for reproductive isolation, which plays a critical role in maintaining species diversity. However, until we understand the relative contribution of reproductive isolation (and other factors) (Table 1) to taxonomic speciation rates, we cannot claim to have answered the most basic questions about the diversity of life that surrounds us. Today, more than 150 years after the publication of the *Origin of Species*, I believe that we understand rather less than we typically think about the processes that created Darwin's Entangled Bank, 'clothed with many plants of many different kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth' (Darwin, 1859: 489). However, there is no better time than the present to apply the set of methodological and theoretical tools currently at our disposal to the full spectrum of speciation rate controls.

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