

Perspective

Common misconceptions of speciation

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ABSTRACT

Speciation is a complex process that can unfold in many different ways. Speciation researchers sometimes simplify core principles in their writing in a way that implies misconceptions about the speciation process. While we think that these misconceptions are usually inadvertently implied (and not actively believed) by the researchers, they nonetheless risk warping how external readers understand speciation. Here we highlight six misconceptions of speciation that are especially widespread. First, species are implied to be clearly and consistently defined entities in nature, whereas in reality species boundaries are often fuzzy and semipermeable. Second, speciation is often implied to be 'good', which is two-fold problematic because it implies both that evolution has a goal and that speciation universally increases the chances of lineage persistence. Third, species-poor clades with species-rich sister clades are considered 'primitive' or 'basal', falsely implying a ladder of progress. Fourth, the evolution of species is assumed to be strictly tree-like, but genomic findings show widespread hybridization more consistent with network-like evolution. Fifth, a lack of association between a trait and elevated speciation rates in macroevolutionary studies is often interpreted as evidence against its relevance in speciation—even if microevolutionary case studies show that it is relevant. Sixth, obvious trait differences between species are sometimes too readily assumed to be (i) barriers to reproduction, (ii) a stepping-stone to inevitable speciation, or (iii) reflective of the species' whole divergence history. In conclusion, we call for caution, particularly when communicating science, because miscommunication of these ideas provides fertile ground for misconceptions to spread.

Keywords: speciation; misconception; miscommunication; diversification; species; taxonomy

INTRODUCTION

Speciation is a complex, multifaceted process in the evolution of biological organisms. The complexity of speciation means that miscommunication of core principles can occur when researchers oversimplify these ideas in their writing. The multifaceted nature of speciation, meanwhile, means that a combination of diverse approaches (genomic, behavioural, macroevolutionary, developmental, etc) is required to understand it. Researchers focusing on different approaches often have differing views of speciation (Stankowski *et al.* 2024), and tend to focus on some aspects and oversimplify others—again raising the potential for miscommunications. Here, we would like to highlight a few misconceptions of speciation that we (and others) have observed (Fig. 1). In most cases the speciation researchers do not actively believe these misconceptions and instead the researchers (including ourselves!) inadvertently imply one or more misconceptions

through their writing or presentations. This risks warping how external readers, including students, understand speciation. But we also suspect that the frequent repetition of statements that imply a misconception sometimes causes researchers themselves to internalize and propagate that misconception—even if they would readily acknowledge the misconception upon closer consideration. Deliberate or not, these miscommunications continue to appear in the speciation literature and in teaching and we risk having our outlook and priorities warped by them. We therefore call for researchers to keep them in mind while designing projects and communicating our research. While we are not the first to identify these misconceptions, by discussing them together here, we hope to raise awareness about them, to highlight how they interact with one another, to underscore how important they are to resist, and to provide a cautionary resource to those new to the field of speciation.

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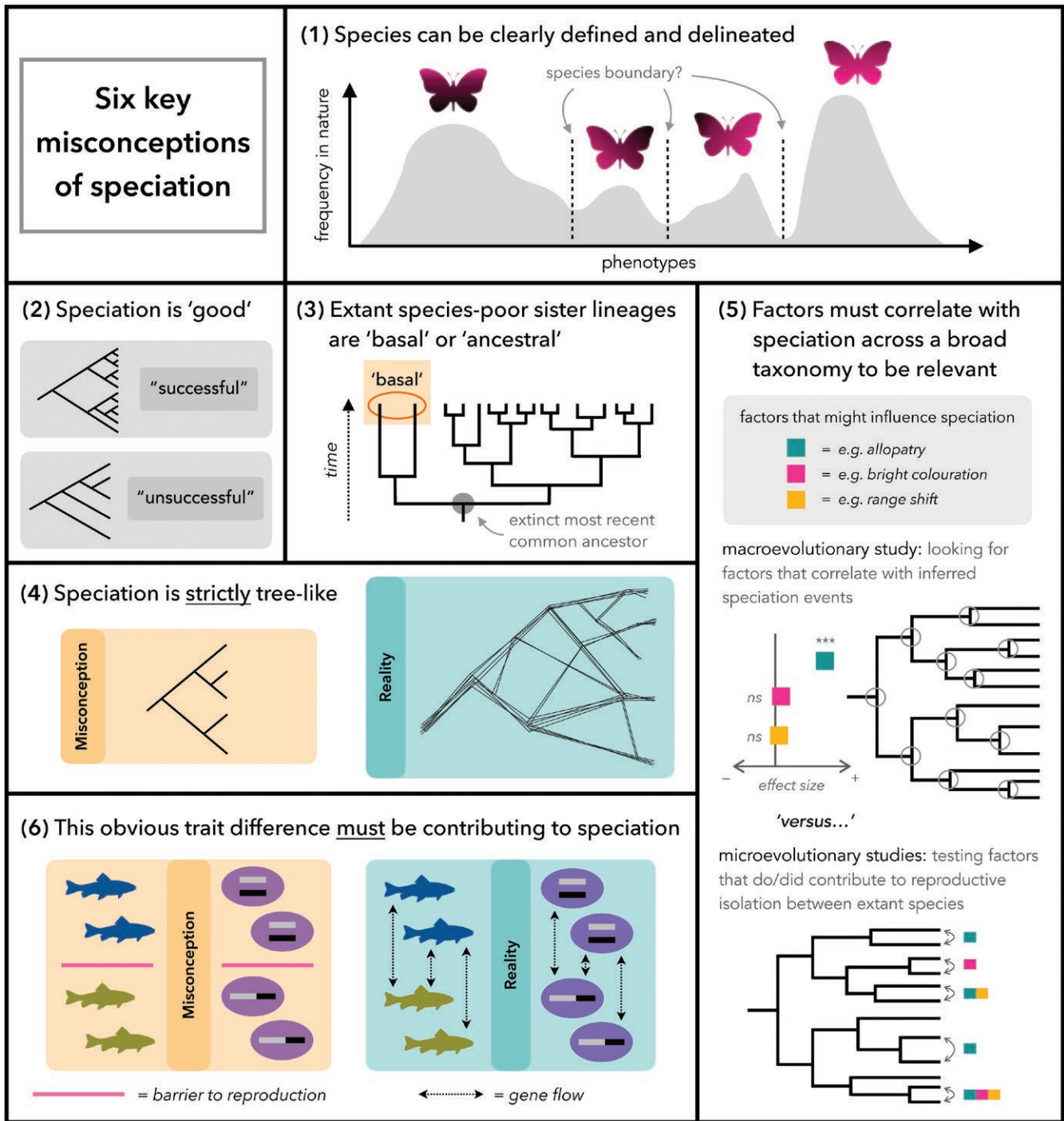


Figure 1. Six common misconceptions of speciation that are discussed in this perspective. (1) That species are clearly and consistently defined and delineated in nature, whereas in reality they are fluid arbitrary taxonomic constructs with fuzzy and semipermeable boundaries. (2) That speciation is inherently ‘good’ or the only route to evolutionary ‘success’, whereas speciation is neither goal-oriented nor the only route to ‘biological success’ however that is measured. (3) That species-poor lineages which are sister to species-rich lineages are ‘lesser’, ‘basal’, ‘ancestral’, or ‘primitive’, whereas in reality no extant lineage can be ancestral to another extant lineage and slowly speciating lineages are equally worthy of research attention as fast-speciating ones. (4) That speciation is strictly tree-like as a process and pattern, whereas genomic results reveal that it commonly appears to be network-like. (5) That factors must correlate with speciation across a broad taxonomy (in macroevolutionary studies) in order to be relevant to speciation, whereas microevolutionary studies of species pairs might reveal different factors as relevant and this should complement (and not be overruled by) the results of macroevolutionary studies. (6) That obvious trait differences between species or populations must be contributing to reproductive isolation, be a precursor to future speciation, or reflect the whole history of their divergence.

(1) 'SPECIES CAN BE CLEARLY DEFINED AND DELINEATED'

A common misconception of those outside the speciation field is that species have a clear definition and can be consistently and robustly delineated. This misconception has been discussed extensively in the literature (Mayr 1970, Cracraft 1989, Hey 2001, Coyne and Orr 2003, Mallet *et al.* 2024) and is well-versed among speciation researchers. We do not intend to regurgitate the existing discussions at length, but we will briefly lay out the core issue for the benefit of those new to the field and because a list of misconceptions of speciation would be incomplete without it.

There is no unified, consistent, or clear-cut concept or working definition for species that all speciation researchers use. Ultimately this derives from the fact that natural diversity is not organized into clear-cut boxes of individuals with unambiguous ecological, phenotypic, or genetic divisions between them. This is, in part, a consequence of most speciation processes not being instantaneous. Any process of divergence that is protracted over long time periods necessarily implies that the boundaries between 'species' are fuzzy in many cases. In other words, even if the label of 'species' is helpful in describing patterns of divergence that have evolutionary significance, no amount of agreement over species concepts and definitions can overcome this fundamental constraint.

But even putting this aside, researchers may differ greatly in their views of how to define species in practice. There are many concepts of what 'species' represent, each assigning different importance to various forms of distinctiveness, including ecological, phenotypic, phylogenetic, reproductive, and genetic distinctiveness. And within each concept, researchers working with different taxa or with different approaches might adopt different working definitions in order to delineate species in practice. Some of the concepts have well-known flaws. In many schools, students are taught that species are groups of individuals that can interbreed to produce fertile offspring and that are reproductively isolated from other such groups [the strict 'Biological Species Concept' (Mayr 1970)]. That is certainly true if one compares, say, a penguin and a zebra, but looking at more closely related species, it gets complicated. A definition for species that relies on complete reproductive isolation is incompatible with the widespread occurrence of hybridization between pairs of lineages that can be quite distantly related and are sufficiently ecologically, phenotypically, and genetically distinct that assigning the label of 'species' is useful from an evolutionary perspective. We now recognize that a large proportion of lineages have a history of hybridization with at least one other lineage that is described as a different species (Mallet 2005, Ellstrand 2014). In our view, the important question is not whether hybridization is zero but whether reproductive isolation between two lineages is sufficient that they can coexist without merging due to hybridization. However, many recently diverged taxa have little overlap of distribution ranges and in areas of contact they show intermediate levels of reproductive isolation. Where we set the threshold of 'sufficient reproductive isolation' is arbitrary. To complicate matters further, reproductive isolation can change over time and space and depend on environmental factors. A clear classification into species is thus often not possible.

Diverging lineages are now typically viewed as being somewhere along a speciation continuum (Stankowski and Ravinet 2021). Speciation researchers use a variety of species definitions (Mallet *et al.* 2024), in part because different approaches to study speciation require different definitions. For instance, researchers studying purely allopatric species, asexual taxa, or fossils without DNA remains cannot study levels of admixture. Some concepts explicitly acknowledge that there is no clear dividing line, such as the 'Genotypic Cluster Concept', which proposes that species are fluid and somewhat distinguishable clusters of genotypes whose overlap varies through time (Mallet 2007).

What practical steps can speciation researchers take to resist this misconception forming in the minds of audiences outside the field, when referring to 'species' remains an indispensable component of our work? First, in research articles, we should state the species concept that we are adopting (e.g. ecologically/genetically/phenotypically oriented) as well as the working definition that we are using within that concept to delineate species (e.g. lack of hybrids observed or below threshold genetic similarity). This is especially important when communicating with other speciation researchers. It is possible that no single species concept will ever satisfy researchers from all backgrounds; and it is unlikely that there will ever be a single working definition that is practically applicable for all taxa and research approaches. This was recognized by Darwin (albeit in male-centric language that does not reflect the diversity of naturalists): 'No one definition has satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species' (Darwin 1859, p. 58). We should embrace this flexibility, but doing so requires us to be explicit in this choice in our writing and presentations. In writing this opinion paper, we ourselves are adopting a species concept that centres around identifying genomic and phenotypic clusters of individuals that can persist in sympatry without merging; however, we adopt the (implied) species concept and definitions of other authors when discussing their original research. (Note that the misconceptions that we outline in the remainder of the article occur independent of which concept or definition of 'species' is used.) Second, speciation researchers should be proactive in explaining 'the species problem' to those outside the field, especially to students or policy-makers. The hazy fluidity of species may become intuitive to us, but it is counter-intuitive to most, as humans like neat and clear categories that can be named and sorted. Species are currently also an important taxonomic unit for conservation, even though the importance of ecotypes and biodiversity at different taxonomic levels is increasingly recognized. Lastly, there may be a case for petitioning a change in how school students are taught about species.

(2) SPECIATION IS 'GOOD' AND A LINEAGE MUST SPECIATE TO BE 'SUCCESSFUL'

A common misconception of speciation stems from equating speciation with 'success' and taking the number of species within a lineage as the sole indicator of evolutionary success (Fig. 1, panel 2). This perspective might lead us to view species-rich lineages with elaborate adaptations visible to humans as more 'successful' than species-poor lineages or lineages with less visible trait changes (Kelemen 2012). This outlook presents at least two key issues.

First, evolutionary ‘success’ is a poorly and inconsistently defined notion that could reasonably include lineage persistence, range size, population size, colonizing ability, as well as species richness. Therefore, if the concept of ‘success’ is to be invoked, it cannot simply be equated to speciation rate. It is clear, for instance, that lineage persistence is not simply related to speciation. While speciation can increase biodiversity, it can also make the daughter species more vulnerable to extinction as they may have smaller population sizes and be more specialized and thus less evolutionarily flexible than the ancestral species (Korkeamäki and Suhonen 2002, Davies *et al.* 2004, Dennis *et al.* 2011, Nolte *et al.* 2019). Several ancient lineages, such as lungfish, horseshoe crabs, and coelacanths, have shown remarkable persistence through geological epochs and environmental shifts with relatively little speciation or phenotypic change (Lee *et al.* 2006, Amemiya *et al.* 2013, Nong *et al.* 2021, Fuselli *et al.* 2023, Brownstein *et al.* 2024). Similarly, ecological polymorphisms and generalist lifestyles can lead to niche expansion, increased flexibility in resource use, and more resilience during environmental fluctuations, thereby reducing extinction risks (Cutter and Gray 2016). For instance, even though host plant specialization is thought to be a key driver of speciation in many herbivorous insects (Wheat *et al.* 2007, Fordyce 2010, Katoh *et al.* 2014, McKenna *et al.* 2019), many long-term persistent and widespread species are generalists (Chichorro *et al.* 2019). In sum, speciation does not—on its own—indicate that a lineage is ‘successful’.

Second, equating speciation with ‘success’ can invoke the related teleological misconception that speciation is in some way ‘good’, inherently progressive, and aiming towards specific final goals. This often derives from our tendency to anthropomorphize evolution, attributing human-like conscious intentions to evolutionary processes (Kelemen 2012). These viewpoints influence how we interpret biodiversity—seeing it as a purposeful contribution and a deliberate outcome of speciation. Despite this teleological outlook being well-established as a misunderstanding, it is still reflected in phrases along the lines of: ‘This lineage has managed to speciate many times.’ While anthropomorphizing and teleological thinking is intuitive for us, it can bias our thinking (Kampourakis and Zogza 2008, Coley and Tanner 2015). Whether consciously or subconsciously, adhering to this viewpoint affects how we conduct and interpret research on speciation. For instance, when one assumes that certain traits or properties of organisms evolved for specific purposes, one may disproportionately favour the adaptive explanations for species divergence that are most apparent to human eyes (such as new species evolve to exploit vacant ecological niches). This bias will skew our understanding of how speciation progresses in cases where the most obvious adaptive explanation is either incorrect or only part of the story. Finally, this teleological outlook can lead to the assumption that any structured variation observed within a species (especially ecological) will inevitably lead to speciation; we discuss this misconception in our sixth point below. In practice, evolutionary divergence has no predetermined directionality, and cases of speciation reversal (‘species collapse’) through rampant hybridization are well documented (Seehausen *et al.* 2008, Behm *et al.* 2010, Kearns *et al.* 2018).

In sum, we call for caution to avoid implying a progress-driven narrative that views speciation as inherently ‘good’ or solely

determining ‘success’ and instead write in a way that reflects a more balanced view on the persistence, evolution, and maintenance of lineages. For instance, we should refer to a lineage as ‘rapidly speciating’ or ‘slowly speciating’ rather than being ‘good speciators’ or ‘poor speciators’. Similarly, we should use more precise and less emotive phrases than ‘successful’ when describing a lineage—such as ‘species rich’, ‘rapidly speciating’, ‘ecologically dominant’, ‘evolutionarily persistent’, or having a ‘cosmopolitan distribution’, as appropriate. And, as always, we should be careful not to favour obvious adaptive explanations for diversification but instead give equal attention to all reasonable hypotheses. Similarly, we should avoid focusing only on fast-speciating lineages in our research and also study slowly speciating lineages. For instance, extensive research into the Heliconiini radiation of butterflies has yielded many important insights into the dynamics of speciation (Jiggins *et al.* 2001, The Heliconius Genome Consortium 2012, Wallbank *et al.* 2016, Edelman *et al.* 2019, Rosser *et al.* 2024, Rossi *et al.* 2024). But comparatively little work has investigated the earliest diverging heliconiine lineage, the monotypic genus *Dryas*. *Dryas iulia* is distributed very widely, participates in a mimicry ring shared by other heliconiine butterflies, but has not diversified morphologically in the way that its sister lineages have (Merrill *et al.* 2015, De-Kayne *et al.* 2024). Understanding why not is just as relevant a question as why other heliconiine lineages have radiated.

(3) SPECIES-POOR SISTER CLADES OF RAPIDLY SPECIATING CLADES ARE ‘BASAL’ OR ‘ANCESTRAL’

A third misconception of speciation is that species-poor lineages with more species-rich sister lineages are in some way ‘basal’, ‘ancestral’, or ‘primitive’ (Fig. 1, panel 3). Note that this has much of the flavour of the previous misconception: that slowly speciating lineages are not ‘good’ or ‘successful’ and are therefore ‘lesser’, but here the issue stems from misinterpreting phylogenies. While phylogenies are powerful tools for analysing evolutionary relationships and the evolution of traits, their seemingly simple structure can lead to misconceptions about what they convey. Historically, phylogenies were depicted as a ‘ladder of progress’ with humans as the pinnacle of evolution and even today phylogenies are often misread as being directional and some taxa being less evolved than others. In reality, all extant descendants of a particular ancestor (node) have been evolving equally long. Consequently, an extant species or clade cannot be ‘ancestral’ or ‘basal’ to another extant species or clade—they can only share a common ancestor, making them evolutionary cousins, each with a mixture of ancestral and derived traits (Omland *et al.* 2008, McDaniel 2021).

This mischaracterization is also fuelled by the nature of the biological taxa upon which we focus. Rapidly speciating clades justifiably attract research attention, but their species-poorer sister clades are mostly only included as outgroups. When presented in a phylogeny, the high number of short branches in species-rich clades compared to few, long branches of species-poorer sister lineages could intuitively lead a reader to see a progression from ‘lesser developed’ lineages into the ‘progressive’ diverse clade. This risk is inherent in any unbalanced phylogeny, but it may be exacerbated by the orientation of the tree. For

instance, if the slowly speciating clade is oriented to the left of a page and the rapidly speciating clade to the right, this might further create the impression of a progression from ‘lesser’ to ‘greater’ by readers who read from left-to-right (and vice versa) (Sandvik 2009). Speciation researchers themselves sometimes fuel this misconception through misleading language. Instead of referring to species-poor clades as ‘basal’, ‘ancestral’, or ‘primitive’, we should simply refer to them as ‘sister lineages’ of the species-richer clade. If one wanted to stress that they are much more divergent from the other lineages, one could use ‘distantly related lineages’.

(4) ‘SPECIATION IS STRICTLY TREE-LIKE’

A common misconception is to assume that speciation follows a strictly tree-like process in which one lineage splits cleanly into two (‘bifurcates’) during speciation forming two isolated daughter species (Mallet *et al.* 2016). An alternative perspective is that speciation is a network-like process in which species can have more than two parental lineages. Lineages accumulate reproductive isolation from one another slowly. Non-sister lineages (that are sometimes already very divergent) may still interbreed, and this genetic exchange can enrich the genetic diversity and further fuel speciation. In reality, speciation can unfold via both tree-like and/or network-like processes and typically generates both tree-like and network-like patterns (Fig. 1, panel 4). The exact balance of tree-like and network-like processes probably varies substantially between lineages and remains a central open question in speciation research. This is recognized broadly within the speciation literature, but the misconception persists among the wider biological community.

There is compelling evidence for network-like speciation, but we should be very careful to distinguish the process of speciation from the patterns that it generates. If one compares recently diverged taxa, phylogenetic trees inferred from different genomic regions typically differ markedly in topology due to incomplete lineage sorting and gene flow, illustrating a network-like pattern of speciation (Mallet *et al.* 2016). For instance, in the species-complex of *Anopheles* mosquitoes, only about 2% of the genome with the deepest coalescent times (on the X-chromosome) aligns with what might be traditionally termed the ‘species tree’ while the remainder of the genome yields a conflicting majority phylogeny (Fontaine *et al.* 2015). It is sometimes believed that obtaining a tree inferred from a large enough number of genes would overcome rare ‘incorrect’ topologies and reveal the ‘true’ phylogeny. But it is now clear that even if a ‘true’ phylogenetic tree—i.e. a tree that accurately describes how species and populations have branched and evolved—does exist: (i) it would probably not be strictly bifurcating, and (ii) it could be entirely obscured by genuine network-like patterns in the genome. It is here that we should distinguish *pattern* from *process* clearly. Genomes are a mosaic of evolutionary ancestries because of several complex processes that include: incomplete lineage sorting (in which ancestral polymorphisms persist between speciation events); gene duplication; gene loss; introgressive hybridization (in which lineages with different genomic ancestries produce fertile hybrids, thereby combining genetic material from both lineages and transferring genetic variants between lineages

through backcrossing); and horizontal gene transfer (in which genetic material is passed between individuals that can be very distantly related by some process other than sexual reproduction) (Maddison 1997, Mallet *et al.* 2016, Arnold and Kunte 2017). All of the genomic processes listed above will generate a network-like *pattern* of speciation (i.e. discordant gene trees), but they do not necessarily represent a network-like *process* of speciation. For instance, a perfectly tree-like process of speciation—such as one population splitting perfectly in two due to a geographical isolation and evolving in complete separation into two species—will at least initially still show network-like patterns at the genetic level due to incomplete lineage sorting, gene duplication, and gene loss.

This caveat aside, it has become increasingly clear that truly network-like processes—such as hybridization between distant lineages fuelling speciation—are in fact common in nature. For instance, the high level of discordance in *Anopheles* mosquitoes is due primarily to rampant ongoing hybridization between species (Fontaine *et al.* 2015). The increasing availability of genomic sequencing has shown that this phenomenon is widespread across the whole tree of life (Ellstrand 2014). Even in classic cases of allopatric speciation amongst *Drosophila* species pairs, there is extensive evidence for past gene flow between sister taxa (Yusuf *et al.* 2024) and gene exchange between more distant relatives (Suvorov *et al.* 2022).

Perhaps the most striking illustration of a network-like speciation process comes from cases of hybrid speciation in which a new species emerges as a direct consequence of hybridization between two distinct lineages (Schumer *et al.* 2014). In these cases, one lineage is the daughter of two parental lineages coming together (Rieseberg *et al.* 2003, Rosser *et al.* 2024). Hybrid speciation illustrates that gene exchange, particularly between non-sister taxa, introduces new genetic variants and generates novel combinations of genetic variants that can be beneficial. Under certain conditions, gene exchange can thus facilitate adaptation, reproductive isolation, and therefore ‘combinatorial speciation’ (Rieseberg 2006, Marques *et al.* 2019, Rosser *et al.* 2024, Rossi *et al.* 2024)—even whole adaptive radiations (Barrier *et al.* 1999, Seehausen 2004, Meier *et al.* 2017, Marques *et al.* 2019). Importantly, the genetic variants underlying reproductive isolation may by far pre-date the speciation event and thus show much deeper phylogenies or discordance with the species tree if they are introgressed from another species (Marques *et al.* 2019). These cases illustrate that there may be many parental lineages that contribute to an incipient species.

It is also worth briefly noting that the degree to which a phylogeny appears to show a tree-like versus network-like pattern depends on the resolution of the study. At one extreme, if many representatives of multiple populations of several closely related species are included in a phylogeny, then network-like patterns will probably be particularly widespread. At the other extreme, if only a single representative of each genus across an order of organisms is used, then tree-like patterns of trait and gene evolution are likely to dominate across speciation events. This is because hybridization is most common among closely related lineages and if one compares only very distantly related lineages, the fact that each of those distantly related lineages may hybridize with its close relatives will not be visible. In addition,

network-like patterns are expected to be lost over evolutionary time due to lineage sorting or because they become harder to detect due to high divergence of homologous sequences. Adding more closely related individuals increases the effective temporal resolution and thus increases the power to detect network-like patterns across speciation events.

There are several practical consequences of accepting a network-like speciation process. The observation that the evolutionary history of lineages should instead be thought of as a complex ‘web’ or ‘network’ in which different regions of an individual’s genome can have greatly different histories is now widely acknowledged by researchers working on young species complexes (Mallet *et al.* 2016). But it is still sometimes lacking from discussions of deeper nodes and this could have important knock-on consequences. For instance, the reconstruction of trait evolution across phylogenies or the inference of speciation rates is based on a phylogeny assumed to be correct. New methods need to be developed to account for the network-like reality of evolution.

Similarly, the web-like evolution of species has practical implications in taxonomy because it can also challenge the taxonomic requirement for species to be monophyletic [*sensu stricto*, common ancestor and all its descendants (Hennig 1974)]. If some populations of a species hybridize with another species, they can become genomically more similar to that species than to conspecific allopatric populations. For instance, *Heliconius elevatus* and *H. pardalinus* in the Amazon are more similar genomically to each other than to their allopatric conspecifics (Rosser *et al.* 2024). Similarly, if a new species evolves from a population in a subset of the range of another species, it may be temporarily nested within the clade of its sister species [e.g. *Heliconius himera* is nested within *H. erato* (Kozak *et al.*, 2021)]. Different parts of the genome can have different origins, potentially including multiple ancestral species. Thus, when an observer attempts to define a species by enforcing a strict monophyletic criterion, they are compelled to ‘choose’ one of the various ancestral origins as the sole acknowledged ancestor of the extant taxa. This approach obscures the reality of multiple ancestries across a species’ genome, underscoring the inadequacy of the tree-like model as the only possible reflection of a species’ evolutionary history. This perspective has been recognized for several years (De Queiroz 2007, Hörandl and Stuessy 2010) but this recognition is still not widespread in systematics and evolutionary biology. This is partly due to the difficulty of fitting reticulate models to large datasets due to computational challenges (Morrison 2014) and partly due to a prevailing sentiment within the wider scientific community that favours the ease of a ‘clean’ and stable independent evolutionary history for a taxon to be recognized as a species.

(5) ‘IF A FACTOR IS NOT CORRELATED WITH SPECIATION ACROSS BROAD TAXONOMIC GROUPS, IT IS NOT RELEVANT’

This particular misconception is usually expressed as follows: ‘Factor X has been found to play an important role in the divergence of species A and B, but factor X is not correlated with speciation rates across their genus/family/order; factor X is

therefore not relevant to speciation.’ For instance, microevolutionary studies demonstrate a clear importance of allopatric divergence in specific cases of vertebrate speciation (Hare *et al.* 2002, Coyne and Orr 2003, Hoskin *et al.* 2005, Black *et al.* 2024), yet this is not reflected at a macroevolutionary level (Anderson and Weir 2022)—and some might be tempted to conclude that allopatric divergence is therefore not relevant in speciation (Fig. 1, panel 5). Note that factor X in the statement above might be a process (such as sexual selection or hybridization), trait (phenotypic or genomic), or environmental condition (biotic or abiotic). By ‘macroevolutionary’ studies, we are mostly referring to phylogenetic comparative approaches across broad taxonomic groups including many species, and we refer to studies comparing individual species pairs as ‘microevolutionary’ studies in this context.

There are at least three potential flaws in the logic invoked by this misconception. First, the present-day distribution of traits across a phylogeny may not be informative of which evolutionary changes were important historically in driving the origin of species at the moment of their divergence or isolation. Second, we should be very cautious when inferring evolutionary processes from patterns of trait evolution. For instance, whether or not sexual selection is recovered as a significant predictor of speciation rates in large clades can depend entirely upon which traits one uses as a proxy for sexual selection (Kraaijeveld *et al.* 2011, Cally *et al.* 2021). Evolutionary processes, such as sexual selection, may act on different traits in different lineages, and the processes could therefore manifest in diverse and unexpected forms. Thus, a trait not being correlated with speciation rates in a taxon is insufficient evidence to claim the trait plays no role in speciation in that group. In sum, macroevolutionary studies aim to find broad-scale associations and if they do find any, they are likely to be meaningful; however, absence of a correlation should not be over-interpreted.

Third, even if a factor does not appear to be relevant when averaged across the whole group, it may still have been important in many individual speciation events within that clade. Speciation is a mosaic of many interacting evolutionary processes whose relative importance may vary greatly between closely related species depending upon their natural history, developmental constraints, and genomic background. Indeed, we should not expect a priori that all lineages within taxonomic groups will undergo similar speciation processes at all because they may differ in natural history, biogeographical setting, strengths of selection on different traits, and so on. The result is that taxonomic groups (from domains down to genera) are likely to exhibit a myriad of speciation mechanisms and none of those mechanisms should be dismissed simply because they are not frequent enough to be detected by macroevolutionary analyses within diverse clades. This principle is obvious when considering the largest taxonomic groups. A higher tolerance for polyploidy in plants and fungi than animals, for instance, makes polyploid speciation far more widespread in plants and fungi (Wood *et al.* 2009)—but its rarity among animals does not make it less relevant to eukaryotic speciation as a whole (Muller 1925, Mable 2004). At lower taxonomic levels, life history can still vary to a great enough degree that different factors drive speciation within younger clades. For instance, while tight pollinator–flower coevolutionary

relationships appear to be important in the speciation of some angiosperm lineages (Bradshaw and Schemske 2003), pollinator syndromes are too diffuse when averaged across large plant clades for this alone to be a widespread explanation for angiosperm diversity (Ollerton *et al.* 2009). Similarly, microevolutionary studies have demonstrated that sexual selection is a critical component of many instances of speciation (Mendelson and Safran 2021, Turbek *et al.* 2021). And yet, macroevolutionary studies are equivocal on whether there is a link between sexual selection and speciation: Ritchie (2007) concludes that ‘the evidence for an effect of sexual selection on speciation is not overwhelming’. It is inevitable that when we sum across many lineages with diverse biologies, we will dilute the apparent importance of factors that are critical in driving individual cases of speciation.

We are not arguing that the findings of macroevolutionary speciation studies should be discounted in the light of microevolutionary studies—quite the opposite. These two approaches are complementary and ask different questions. Microevolutionary studies test precise hypotheses in a narrowly defined taxonomic and environmental context, while macroevolutionary studies look for informative general trends across huge spatial and taxonomic breadth, make comparisons between very different lineages, and test patterns of diversification through time. We therefore make two proposals to help overcome this misconception. First, we should not be surprised if these two approaches reach different conclusions about speciation within a particular clade—and those different conclusions do not mean that they are in conflict with one another. Instead, we should frame macro- and microevolutionary studies as complementing one another rather than conflicting. And second, macroevolutionary studies should be interpreted within the context of the taxa’s natural history and the idiosyncrasies of particular lineages must not be lost in the weeds. Even within a single genus, speciation may differ greatly from lineage to lineage according to their biology, as illustrated by marine snails (Johannesson *et al.* 2024).

This misconception is occasionally accompanied by a further misconception: that ‘if a factor is strongly correlated with speciation in a group then all other factors are irrelevant’. However, speciation is a long and multifaceted process with many interacting components that will change in importance at different moments in the speciation process. For instance, it is the combination of ecological opportunity, ecology-linked sexual diversification, and high genetic diversity due to hybridization that explains the rapid adaptive radiation of some East African cichlid fishes (Meier *et al.* 2019). Similarly, diversification in the species-rich family Orchidaceae (orchids) is attributable to traits implicated in ecological divergence (CAM photosynthesis and epiphytism) and sexual divergence (pollinia and pollination by bees and Lepidoptera), as well as with environmental factors (tropical regions and cordilleras) (Givnish *et al.* 2015). We would benefit from embracing this complexity and viewing all of these interacting factors as highly relevant.

(6) ASSUMPTIONS MADE ABOUT THE LINKS BETWEEN TRAIT DIFFERENCES, BARRIERS, AND DIVERGENCE BETWEEN SPECIES

Speciation involves the accumulation of barriers to gene flow that progressively increase the reproductive isolation (RI) of lineages

(Coyne and Orr 2003). Characterizing the nature and timing of these barriers and their impact on gene flow is therefore a fundamental goal of speciation research. However, a common misconception—often made by those outside the speciation field—is to make assumptions about the relationship between three distinct things: patterns of trait differences, patterns of barriers to reproduction, and the process of divergence. These assumptions generate three varieties of the same misconception: in the present, future, and past tenses (Fig. 1, panel 6).

(6a) *Present tense: ‘This obvious trait difference between species must be a barrier to reproduction’*

The first variety of the misconception is the assumption that all traits that distinguish species from each other today are probably acting as species barriers. Barriers do indeed maintain diagnostic traits in distinct species, but not all diagnostic trait differences between two species are barriers. Some differences may have accumulated after speciation or are genetically linked to another trait contributing to reproductive isolation and thus experiencing reduced gene flow. Furthermore, barriers are not universal and a trait that acts as a barrier between two species may not be a barrier between a different pair of species or even between different populations of the same species (Harrison and Larson 2016).

The misconception that species differences are always barriers to gene flow potentially originates from species being classified by their observable differences (Linnaeus 1735, Darwin 1859). In some cases, those species-defining traits are indeed contributing to RI: colour differences in the Italian sparrow (*Passer italiae*) and house sparrow (*P. domesticus*) (Elgvin *et al.* 2011), habitat divergence in *Cottus* sculpins (Stemshorn *et al.* 2011), prezygotic barriers between *Mimulus* spp. flowers (Bradshaw and Schemske 2003), and chromosomal differences in *Brenthis* butterflies (Mackintosh *et al.* 2023). But the traits that act as barriers in these examples need not be barriers between lineages in other situations. For instance, although white wagtail subspecies (*Motacilla alba alba* vs. *M. a. personatus*) differ consistently in colour on their head, neck, wing coverts, and back, only head traits are involved in RI between them (Semenov *et al.* 2017). Similarly, when species that differ in many traits are brought into secondary contact, it is often observed that a subset of those traits introgresses rapidly between the species, indicating that they make no or only minor contributions to RI and are thus overwhelmed by gene flow. This has been reported widely in plants (Suarez-Gonzalez *et al.* 2018) and animals (Hedrick 2013). In summary, obvious trait differences between species—such as chromosomal rearrangements, colour patterns, pheromones, and ecological niche—are commonly perceived as barriers but may have no impact on RI.

(6b) *Future tense: ‘This trait difference/barrier between individuals will inevitably lead to a future increase in reproductive isolation’*

The future variety of this misconception is that trait differences between individuals—whether or not they are barriers to reproduction—are precursors to an inevitable future increase in RI and will always lead to complete speciation. This misconception is most apparent in the case of polymorphisms—defined as the co-occurrence of multiple discrete, heritable morphs within populations (Ford 1945, De Solan *et al.* 2023). Polymorphisms

are sometimes automatically assumed to be a stepping stone towards further increased RI, divergence, and speciation without evidence to support this view. It is important to distinguish that even though polymorphisms can provide the raw material for diversification (Drès and Mallet 2002), their presence does not necessarily imply RI between morphs (Jamie and Meier 2020). And critically, even if there is a degree of RI between morphs, that does not mean the morphs will inevitably evolve into distinct lineages that we decide to designate as species in the long run. This misconception has a teleological flavour, suggesting that divergent polymorphisms have speciation as a specific goal (see the second misconception discussed above). It has existed for many years, with Wallace (1865) describing polymorphism as the initial stage of divergence in his six-stage model (Stankowski and Ravinet 2021). However, many polymorphisms are found in many different species and maintained in both daughter species after speciation, indicating that they did not contribute to speciation (Jamie and Meier 2020). In some cases, the morphs are maintained by disassortative mating (preferential mating with the other morph types) and are thus unlikely to contribute to RI. The most obvious example is sex in species that exhibit genetically determined males and females. Similarly, long-term balancing selection has maintained head colour pattern variation in the Gouldian finch (Toomey et al. 2018, Kim et al. 2019) and the three male morphs of the ruff (Baguette et al. 2022) without leading to RI. Divergent colour morphs were thought to lead to speciation in *Heliconius numata* butterflies and in *Timema cristinae* stick insects, but later studies have shown that mating preferences and natural selection appear to counteract ecological speciation (Chouteau et al. 2017, Nosil et al. 2024). In the butterfly *Leptidea sinapis*, the karyotype difference is larger within species ($N = 24-53$) than between closely related species (Lukhtanov et al. 2011), demonstrating that chromosomal differences do not inevitably lead to speciation.

We caution here that it is very challenging to predict if trait differences will contribute to complete RI between species. On the other hand, it is also not possible to exclude that they will (Butlin and Faria 2024). Weak barriers may become coupled (i.e. coincide with each other) and together result in strong barriers (Butlin and Smadja 2018). For instance, in the European corn borer (*Ostrinia nubilalis*) in North America, divergence is greater and more widespread in the genome between populations where both temporal and behavioural barriers coincide compared with populations that differ in only one barrier trait (Dopman et al. 2010, Kunerth et al. 2022). Similarly, in the Midas cichlid fishes, divergence in lip size alone has occurred without genetic divergence in some lakes, but in other lakes this trait was associated with RI in combination with differences in other traits in pharyngeal jaws and body shape (Kautt et al. 2020). And in mice and shrews, simple Robertsonian fusions (in which the long arms of two different chromosomes become fused and the small arms are typically lost) are less likely to lead to complete RI compared with multiple and complex rearrangements (Garagna et al. 1989). The barriers to gene flow have to be strong and widespread enough to maintain the distinct characteristics of the populations in order to result in complete speciation and to prevent species collapse on secondary contact.

(6c) *Past tense: 'This trait difference/barrier between species must have played a role in their initial divergence'*

Finally, a misconception sometimes arises when an observed contemporary trait difference and/or barrier between two species is assumed to have played a role in their past divergence. In reality, the evolutionary forces operating on a lineage vary over time and space. The processes, barriers, and traits that were relevant at some past time point are not necessarily the processes, barriers, or traits that we can observe today. For instance, consider two lineages that were geographically isolated and attained high levels of reproductive isolation during allopatric divergence. If they then came back into secondary contact much later, they might diverge further in other traits unrelated their initial divergence, for example due to reinforcement of reproductive isolation (Hopkins 2013), ecological character displacement (Brown and Wilson 1956), or simply drift and low levels of gene flow. In either case, their new geographical distribution and the traits that now contribute to RI between the two species may not reflect the processes and traits that influenced the earlier allopatric stage of their divergence.

To summarize these three related misconceptions: trait differences between species are not always barriers to gene flow, current differences do not necessarily lead to a future increase in RI or complete speciation, and the barriers that we observe between species today may not reflect the barriers that were key during earlier divergence. Going forward, we advocate for speciation researchers to be proactive (in their writing and presentations) in distinguishing clearly between the *patterns* that we observe in nature when comparing different lineages from the speciation *processes* that have generated those patterns and refrain from strong predictions about how current species differences contribute to future or past reproductive isolation. Awareness of these considerations has great practical importance because this misconception could result in the misclassification of species (Arias-Cárdenas et al. 2024). Lastly, as selection and thus RI can be variable in both time and space, it may be worthwhile to compare species at different places, such as at different hybrid zones (e.g. Westram et al. 2021) or population pairs (e.g. Kunerth et al. 2022, Nosil et al. 2024).

WAYS FORWARD

In writing this perspective piece, we aimed to highlight several misconceptions surrounding speciation that both exist outside of the speciation research community and that speciation researchers (including ourselves) have implied in conversations and written work, inadvertently or not. We are certainly not the first to identify these misconceptions. But we hope that by reviewing them here, we will have illustrated how important they are to resist and how they interact with one another. We think that an awareness of these misconceptions helps to reduce their occurrence, and that helpful proactive steps can be taken in the research community to push back against them. For instance, stating explicitly how species are delineated in our particular study system when we describe them will both acknowledge the imperfectly defined nature of species and make communication between researchers working on different systems easier (misconception 1). A greater focus on the causes and

biodiversity consequences of species persistence can rewire our misperception of speciating lineages as the most ‘successful’ or having achieved a ‘goal’ (misconception 2). An increased focus on the evolutionary dynamics of slowly speciating lineages that are sister to diverse radiations will counteract their perception as ‘basal’ or ‘ancestral’, as well as providing contrast against the better studied radiations (misconception 3). Appropriately conducted genomic analyses with explicit tests for gene exchange should guard against phylogenies being viewed as strictly tree-like (misconception 4). Ensuring that speciation studies are rooted in a strong understanding of the focal species’ natural history will prevent the overlooking of important lineage-specific processes (misconception 5). And adopting multidisciplinary approaches that integrate experimental, behavioural, sensory, and genomic methods to study speciation will counteract assumptions that certain trait differences will inevitably contribute to speciation (misconception 6).

Also critically important is that speciation researchers prevent miscommunication that fuels these misconceptions in teaching and public outreach. While some extent of simplification is required when teaching and communicating with non-specialist audiences, we risk extending the generational lifespan of those misconceptions. Policy-makers and conservationists who view phylogenies as tree-like, species as clear-cut, or members of species-rich lineages as more important in maintaining ecosystems will not make well-informed decisions. Promoting an accurate framing of species and speciation benefits both us and the downstream users of our research.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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