# The macroecology of coexistence

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I, Bouwe Rutger Reijenga, confirm that the work presented in my thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis

# Abstract

Ecological communities are assembled through ecological, environmental and historical processes. Ultimately, evolutionary historical processes, such as speciation and colonisation, are fundamental to assembly, as only speciation generates diversity. Despite history's importance, it is frequently seen as stochastic and contrasts predictability. Here, I investigate this stochasticity and unpredictability.

First, I investigate how the evolutionary history of allopatric speciation and colonisation time influences contemporary communities. I develop and fit a model of community assembly to passerine clades. The clade-specific history of speciation strongly impacts the build-up of sympatric diversity, and phylogenetic tree shape explains a significant proportion of variation in sympatric diversity.

Assembly time is thus important, but is modified by ecological interactions and niche differentiation. Niche differentiation may facilitate sympatry, but when differentiation happens relative to secondary sympatry is unclear. I investigated whether niche differentiation happens before or after sympatry by studying the elevational differentiation of montane avian sister species. Utilising Markov models, I show that the processes occur at equal frequency, and emphasise that niche divergence events constrain the build-up of sympatric diversity.

Lastly, evolutionary history and ecological interactions are integrated in a theoretical model. The model shows that stochasticity in species arrival order in communities can lead to unpredictable variation in local composition, but it does not impact the outcome of species diversification. This highlights that historical effects on one scale do not necessarily result in unpredictability on larger scales.

Taken together, I show how combining phylogenies and process-based models can shed new light on how evolutionary history of lineages and interactions can shape community assembly. While history acts in various ways and over distinct scales, history is not always unpredictable. History has a much greater impact on present-day communities than appreciated, and a re-appraisal of how we view the consequences of history for community and macroecology is necessary.

# Impact statement

The primary goal of the research presented in this thesis was to expand and better our understanding of the key fundamental processes that have shaped the generation and maintenance of biodiversity. The benefits of this research will consequently primarily be found within future academic scholarship, and the main beneficiaries will be other scientists. In addition to the insights I have provided, I have presented multiple new tools, which are publicly available and can be used to continue and answer questions relating to biodiversity science. These methods can help with interpreting data and therefore facilitate the collection of data by encouraging the answering of questions that were previously not addressable.

Although the immediate implications concern the expansion of our understanding of natural phenomena, the results and approaches presented in this thesis may have future applied implications. First, the models that highlight how arrival order in ecological communities could influence the spread and expansion of species may offer important insight in how diseases or invasive species spread **(Chapter 4)**. On the one hand, current disease ecological models do not take into account that competitive interactions between species could influence the spread of disease and consequently influence zoonotic spill-over events between different populations or species. On the other hand, invasive species may have difficulty establishing in areas where competitors profit from priority effects. Knowing how to facilitate these effects might be beneficiary to combat invasive species. Second, my work showed how eco-evolutionary dynamics have resulted in the build-up of tropical montane diversity **(Chapter 3)**. These predictions focus on processes acting over millions of years. However, the observation that species rarely shift up- or downslope over these time scales may have implications for how biodiversity will be suffering under anthropogenically driven climate change. Therefore, the research presented here might indirectly benefit public health concerns, prevention of invasive species, or species extinction, and has the potential to offer new insight in these key challenges.

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# Thesis outline of contents and collaborators

### Chapter 1

#### *General introduction*

In the first chapter, I introduce the framing of the subject matter and highlight the key concepts. I then setup the main questions and gaps in the literature.

### Chapter 2

#### *Evolutionary history explains community diversity and structure*

In the second chapter, I develop an approach to test the impact of evolutionary history on the diversity of present-day communities. This work was carried out in collaboration with David J. Murrell, Rampal S. Etienne and Alex L. Pigot. The idea was conceived by DJM, ALP and myself, after which RE became involved. With input from all co-authors, I devised the approach, carried out the analyses, and wrote the initial draft. This chapter is currently in preparation for submission to a scientific journal.

### Chapter 3

#### *Disentangling the historical routes to community assembly in the global epicentre of biodiversity*

In the third chapter, I aim to understand the relative frequency at which montane avian sister species have assembled through different trajectories. This work was carried out in collaboration with David J. Murrell, Benjamin G. Freeman, and Alex L. Pigot. DJM, ALP and myself conceived of the idea, and I carried out the analyses and wrote the original draft with input from all authors. Additionally, BF performed and provided input on data collection. A version of this chapter is currently under review in a scientific journal, and publicly accessible on bioRxiv under the same title. I further want to express my gratitude to Tim Blackburn for letting me borrow his field guides. This work was presented during: AOS 2021, SSE 2022, and BES 2022.

### Chapter 4

#### *Priority effects and the macroevolutionary dynamics of biodiversity*

In the fourth chapter, I investigate the importance of arrival order on the generation and maintenance of biodiversity. This work was carried out in collaboration with David J. Murrell and Alex L. Pigot, as we together conceived of the idea. I developed the approach and wrote the paper. All authors provided feedback throughout. I further want to express my gratitude to J. Day, A. Phillimore, T. Price, J. Stroud, and G. Thomas for kindly providing opportunities for discussion. This paper has been published in *Ecology Letters* under the same title. This work was presented during the following conferences: SSE 2021, BES Macroecology SIG 2021, ECBC 2021, and ProgPal 2021.

### Chapter 5

#### *General discussion*

In the final chapter, I synthesise the overall key findings of the different studies. I reflect on how the findings fit into the broader disciplines of community ecology, macroecology and macroevolution. I close by outlining future directions and outstanding questions.

### Appendices

#### *Appendix 1*

Supplementary material for Chapter 2.

#### *Appendix 2*

Supplementary material for Chapter 3.

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Supplementary material for Chapter 4.

Chapter 1:

# General introduction

Take any locality on the face of the Earth, a mountain slope of the Andes, an island in the Galapagos, or a patch of Fynbos in South Africa, and the same questions can be asked about the species that occur there. Why are there so many or so few? Why is it that these particular species occur there? And, what allows them to live together? Over the course of the 20th century, community ecology has focused on synthesising answers to these questions. Yet at the end of the last century, Lawton (1999) stated that "community ecology is a mess". Lawton argued that because of the many context-dependent exceptions – contingencies as he put it – to any proposed law, generalisations are difficult or ineffective. The development of macroecology and trait-based approaches has since resulted in significant progress (Kraft *et al.* 2015; McGill 2019; Mittelbach & McGill 2019). However, the sense that Lawton's "mess" has not been entirely cleared up and never will persists, because the inherent historical nature of communities and the resulting contingency, means that predicting the structure, diversity and future of ecological communities will always be a major challenge.

History in general might matter for community assembly based on two key processes. The first consideration is that communities of species that occur together in space are assembled over time (De Meester *et al.* 2016). In many ecological perspectives on community assembly where interspecific ecological interactions (e.g. competition, predation, and mutualism) and environmental conditions together shape which species can persist at a site, it is implicitly assumed that species arrive in parallel. This results from perhaps the most common metaphor of community assembly where assembly acts as a abiotic and biotic filter, resulting in a subset of species being present locally (HilleRisLambers *et al.* 2012). While it could be that species arrive at once, or over a relatively short time span, it is unlikely that arrival is always in parallel. The second consideration is that species pools are often threated as being static (Mittelbach & Schemske 2015). In other words, the species that are available to colonise the community are constant over time and do not change. In reality, species pools might fluctuate over time by speciation, extinction and colonisation (Ricklefs 1987), and species might therefore arrive sequentially.

The temporal component of community assembly stretches further than the arrival of species, as communities fluctuate through time. For instance, the composition of communities can change with the seasons as species migrate (Giovannoni & Vergin 2012). Abundances of populations change from year to year due to drift and fluctuations in resource availability, and this fluctuation might result in local extinction (Hung *et al.* 2014). Over longer time scales, communities gain species through colonisation and speciation, and lose species diversity through extinction (Ricklefs 1987). Ecological niches in a community can become vacant through these extinction events, evolve through time, and impact ecosystem functioning (Valentine *et al.* 2008). The order and timing of these dynamic changes and historical events can ripple through time, shaping both the current and future generation and maintenance of diversity. Therefore, to understand community assembly we need to understand its history, the study of the past events leading to the present.

For community assembly, history can be summarised in two ways: (*i*) What is the order in which events take place (i.e. does A happen before or after B)? And, (*ii*) timing – when do events take place (i.e. how long does it take for A to happen if it happens at all)? Together the order and timing of events have the potential to change and steer community assembly.

A further distinction can be made between the evolutionary history of species and history of the environment in which these species occur. Evolutionary history in this context are the processes that directly impact the composition, structure and species richness. Here, composition is defined as the identity of the species that are present, and structure as the ecological niches that the species fill. Specifically, these processes are the generation of species, global and local extinction, colonisation of the community, and niche evolution. According to the above definition, history could be studied by, for instance, asking if niche evolution happens prior to colonisation (order), or if colonisation of a community happens at all (timing). In contrast, environmental history deals with the factors that shape and drive the evolutionary history of species, including geological events such as mountain-building and the formation of land-bridges, and changes in the climate and weather, from the waxing and waning of ice ages over millions of years to a hurricane. In contrast to evolutionary history, environmental history does not contribute directly to composition, structure or diversity, but modifies the frequency, dynamics and mode of these key evolutionary processes.

Despite the importance of evolutionary history, ecological studies often do not take it into account when studying community assembly. Multiple reasons might have caused this. Researchers may have favoured deterministic ecological models because of their simplicity and predictability, or their focus on contemporary observable and testable processes (Kingsland 1995; Lawton 1999). Indeed, most likely community ecology has not fully taken evolutionary history into account because of the inability to perform experiments beyond a certain time scale. For instance, in many contexts speciation can be safely ignored as it does not tend to happen over ecological time scales, but see (Lamichhaney *et al.* 2018). However, that history seems distant because speciation has happened deep in the past, does not mean that its mark on community assembly is absent.

### History determines which species can be found where

To understand how the species composition of ecological communities has been shaped by history, first envision a world where community composition is not influenced by history. Regardless of history, local communities are subsets of the diversity and species present in the regional pool. At maximum, the local community contains all species that are present regionally but in reality community composition will be guided by environmental filtering and ecological sorting. First, species will be environmentally filtered if their abiotic requirements such as humidity, precipitation, temperature, salinity and acidity are not met (Cadotte & Tucker 2017). For instance, species that are not adapted to the high salinity of salt marshes, or the high temperatures and low precipitation of hot deserts will be absent from those areas. Second, species are sorted ecologically by interactions with other species, including pathogens, predators (Connell 1970; Janzen 1970), mutualists (Chomicki *et al.* 2019), and competitors (Macarthur & Levins 1967). Together environmental filtering and ecological sorting will thus determine the composition of local communities, and cumulatively shape regional species pools.

At first sight, it seems reasonable that the assembly of present-day communities is overwhelmingly determined by ecological and environmental filtering with history playing a minor role: there are no palm trees in the Arctic or Arctic foxes in the tropics. However, in the extreme case, it also clear that this environmentally deterministic world is far-fetched as it would require that local communities are assembled from a single global and homogenised pool of species. While the rapid movement of species around the world by humans is now changing things, the fact that alien species exist today is precisely because prior to humanity, the history of the Earth has had a profound influence in structuring biodiversity.

The idea that history has limited the interchange of species between regions is old and well established in biogeography. In 1876, Alfred Russel Wallace had already proposed a map of terrestrial zoogeographic regions based on the taxonomic relationships between species. Recent developments of molecular taxonomic methodology and advanced clustering methods have refined this demarcation (Holt *et al.* 2013; Ficetola *et al.* 2017; White *et al.* 2019), but the message of these analyses remains the same: zoogeographic and floristic regions contain largely geographically-restricted, evolutionary distinct radiations, resulting in unique community compositions per region.

There are multiple reasons why the biota between these regions have largely remained distinct till this day. The movement of tectonic plates is perhaps most obvious. As distance between regions increases by drift or decreases by the collision of continents, dispersal becomes more difficult due to major geographical barriers arising such as oceans or mountains respectively (Ficetola *et al.* 2017). However, biotic interchanges have happened regularly between different zoogeographic regions, and have had major impacts on the biota of different regions (Vermeij 1991).

The Great American Biotic Interchange (GABI) – is perhaps the textbook example, and has defined the distribution of species across North and South America (Simpson 1980). This interchange, facilitated by the formation of the Isthmus of Panama (Bacon *et al.* 2015), resulted in the northward and southward expansion of North and South American biota respectively. Characteristic of this interchange is the differential extinction of primarily South American species, whereas North American species seemed to thrive in both regions (Carrillo *et al.* 2020). The asymmetry in extinction rate has been associated with competitive superiority of North American lineages (Simpson 1980), predation (Faurby & Svenning 2016), or habitat and environmental change associated with glaciation events (Bacon *et al.* 2016). Regardless of the reason for extinction, the niches that were left open (e.g. by the extinction of the resident South American predators), were filled up by the lineages and descendants arriving from North America (Prevosti *et al.* 2013). Biotic interchanges such as the GABI, where long-established barriers between biotas break down, highlight how the occurrence of historical events have profoundly influenced regional species pools and consequently the composition of present-day local communities.

An equally important consideration here is that the order of events, specifically colonisation and extinction, can directly influence the evolution of regional biotas and thus local community assembly. Specifically, colonisation may drive extinction through an active displacement, or 'push', of the resident species via negative biotic interactions (Silvestro *et al.* 2015). Alternatively, the prior extinction of a species may open up ecological opportunity allowing new species to colonise the region (Jablonski 2001). In other words, rather than extinction being a result of invasion as in the GABI, extinction acts to 'pull' species towards the region (Walker & Valentine 1984). While the outcome of 'push' or 'pull' might be indistinguishable, the distinction between the processes is important for understanding the outcome of which species get replaced and which do not. This therefore offers an example of how the order of events could influence the composition of communities.

The GABI and other interchanges offer a clear example where reconnection between two long separated regions resulted in the intermixing of biodiversity. Yet in other occasions plate movement appears to not change regional composition and by extension local communities. For instance, White et al. (2021) describe how the continental biota of the Southeast Asian Sunda shelf has largely remained separate from the Archipelagic biota of Sulawesi and the Philippines, even though the birds native to the latter archipelagos are highly vagile and could easily cross geographical barriers (White *et al.* 2021). The continued separation of regional biota despite the clear ability of species to colonise the other region has been argued to be the result of the resident species carrying an advantage over invading species that try to establish. This could be caused by their longer residence time and consequently the monopolisation of the available resources or because of negative biotic interactions (e.g. predators or pathogens) experienced by the invader. Thus, even if the present and historical environmental conditions transpire to enable a species to establish in a region and community, it may not be able to depending on the order and timing of arrival – priority effects (Chase 2003; Fukami 2015).

Priority effects are generally discussed as a process that precludes the invasion of any later arriving species or populations (MacArthur 1972). This is caused by populations having attained high population density and occupying the niche that the resident and invading populations or species share, what is often termed niche pre-emption (Fukami 2015). In essence this could thus be described as a "strength in numbers" or density-dependent effect where the early arrivals are exploiting all available resources. For priority effects to be successful, pre-emption needs to be rapid compared to any subsequent invasion. Yet, once populations have successfully established it can be difficult to overturn their incumbency, even when the fitness of invaders is higher. Priority effects may be especially strong if invading species need to adapt to local predators and pathogens (White *et al.* 2021), experience negative density-dependent growth rates (Taylor & Hastings 2005), or if resident species are adapted to available resources (Urban & De Meester 2009). Priority effects may therefore form an important explanation for the maintenance of distinct local community compositions between regions.

Priority effects have likewise been used to explain great turnover between seemingly environmentally and ecologically equivalent communities at smaller spatial scales. Whether species A or species B, that both perhaps occupy the same niche, colonises the community first, will mean that the other species will not be able to establish. Effectively, this may create alternative stable or transient compositional states (Chase 2003; Fukami & Nakajima 2011). Without the historical contingency caused by arrival order and priority effects, it might be difficult to explain high turnover in community composition in highly homogeneous environments. However, under what conditions priority effects operate, when they are strongest, when they act for the longest, and how they could influence the longer term dynamics of biodiversity, including speciation and extinction over macroevolutionary timescales remains unclear.

### History determines the diversity of communities

In a world where history does not matter, in addition to composition, the species richness of local communities would likewise be determined purely by environmental and ecological constraints. In this deterministic world the species richness of communities, after environmental filtering, is limited by the total availability of resources, how these resources are distributed, and how efficiently the species can distribute themselves along these resource axes. Resources here can be interpreted broadly in terms of any factor that limits population growth, including nutrients, shelter, light, water, or space. Each community would be at a diversity equilibrium and disturbances would have no lasting impact on the species present, as the community would rapidly return to equilibrium. Beyond setting a maximum, the total number of species present in the global regional pool would not impact the diversity of local communities which would instead be dictated by environmentally determined carrying capacities.

Many studies have attempted to test the latter prediction, by comparing local community diversity within a given habitat type across regions (Cornell & Lawton 1992). A linear relationship between local and regional diversity was initially interpreted as evidence that historical regional processes (e.g. colonisation, extinction, and speciation) were of greater importance compared to local processes in regulating community diversity (e.g. niche differentiation, and competition) (Terborgh & Faaborg 1980; Ricklefs 1987). In contrast, positive but saturating relationships between local and regional diversity have often been reported and could suggest ecological limits. The implications of these relationships for understanding the role of history in shaping community richness needs to be considered with care. The distinction between regional and local processes is not identical to the distinction between historical and non-historical (e.g. niche differentiation takes place over time), and the interpretation of the local-regional diversity relationship has since developed into a view of "interactive" versus "non-interactive". Here, interactive refers to species interactions limiting coexistence, resulting in a saturating local-regional relationship (Mouquet *et al.* 2003). Furthermore, the mechanistic interpretation of the local-regional richness relationship and the robustness of this simple graphical test has been called into question extensively (Srivastava 1999; Ricklefs 2004).

One particular critique is that local diversity forms part of the regional diversity and cannot be logically separated. Specifically, regional diversity, even in the non-historical world scenario consists of the total diversity of all local communities, and local communities thus automatically bear an imprint of this (He *et al.* 2005). Regardless of the robustness of the test, evidence of interactive and non-interactive communities has been mixed, because some studies, spatial scales and clades show saturating relationships while others do not (Ricklefs 2004; Alroy 2018). Additionally, any linear or saturating local-regional relationship can result from the interplay of stochastic colonisation and extinction of a local community, and thus does not require species interactions to limit local diversity (He *et al.* 2005; Fox & Srivastava 2006). Consequently, the local-regional richness relationship appears to have been mostly abandoned (but see Alroy 2018).

With the increasing availability of molecular phylogenetic data, biogeographic approaches that reconstruct the area in which lineages first arose have been increasingly applied to test how histories shapes current communities. These approaches have the ability to study the timing of first colonisation, and thus how the time available for species to accumulate impacts current richness. Utilising both phylogenetic trees and contemporary geographical distributions, results have suggested that the earlier a region is colonised by a clade, the higher the region's species richness will be (Stephens & Wiens 2003; Wiens 2011). These analyses also find that the higher the regional diversity is, the higher local diversity will be as well (Wiens *et al.* 2011; Wiens 2012). While this shows that the timing of first colonisation can be important for the *in situ* accumulation of diversity through speciation, it does not answer how the unique history of speciation, extinction and colonisation of clades impacts local communities *per se*.

Statistical comparisons of the diversity of particular organismal groups (e.g. mangroves or trees) between regions, have also been used as evidence that regional processes and properties impact local diversity (Ricklefs & Latham 1993). For instance, temperate zone tree genera have twice as many species in eastern Asia compared to the eastern part of North America. This has been attributed to physiographical heterogeneity of eastern Asia in combination with climatic and sea-level changes that have promoted diversification (Qian & Ricklefs 2000). While such studies have focussed on differences in regional diversity, these may in turn constrain local community diversity as well.

Many other examples pertain to particular areas functioning as refugia for environmental catastrophes such as ice ages. For instance, because of the Quaternary climatic fluctuations, coral reef habitat availability has shifted through time. The most species rich present-day communities of reef fish are those that were geographically the closest to refugia (Pellissier *et al.* 2014). Other similar examples exist such as for endemic Andean birds (Fjeldså *et al.* 1999), and tropical tree species (Graham *et al.* 2006). These studies have in common that historical extinction events have decreased diversity, and that colonisation events over time is what again fuels diversity. While these examples highlight that environmental historical events may profoundly determine community diversity, the evolutionary mechanisms that connect these changes to present-day patterns are often not studied.

Over time scales where experiments are possible mechanisms can be evaluated. Specifically, studies have focused on how historical contingency caused by arrival order may influence community diversity. For instance, Fukami et al. (2010) showed via experiments on wood-decaying fungi that depending on which species arrived first, this would determine if more species would be able to colonise the community. This is caused by complex interspecific interactions in which, for instance, *Trametes versicolor* would inhibit *Phlebia nothofagi* from becoming dominant and consequently facilitating *Bisporella citrina*. If *P. nothofagi* would have arrived first, *B. citrina* would have not been able to establish (Fukami *et al.* 2010). The priority effects caused by the wood-decaying fungi are not necessarily inhibitory, as their secondary metabolites can respectively promote and inhibit. Experiments such as these highlight how history can variously facilitate or diminish richness, but extending the implications of these results to broader temporal and spatial scales is challenging.

### History determines the functional role of species within the community

Returning to our world without history for the last time, ponder how the functional roles of species in local communities would be filled. No historical effects means only a single global regional source of species that are present in every local community before filtering and sorting. Species are expected to occur in every local community where they environmentally might be able to sustain themselves. Ecological interactions will sort the community after that. This would lead to deterministic communities where chance does not influence composition, diversity and structure. If competition is the only interaction assumed to structure communities, species with identical ecological niches would likely not be able to exist. If either species has but a slight competitive edge this would lead to the competitive exclusion of the inferior species. Although resource partitioning is primarily used as an example here, niche differentiation may also occur through predator partitioning (Grover 1994; Sedio & Ostling 2013). A specific example of this is the Janzen-Connell hypothesis in which abundant species experience negative-density dependent effects caused by pathogens, herbivores or predators, mediating coexistence of species that show resource overlap (Connell 1970; Janzen 1970). Overall, these dynamics would lead to a very high degree of convergence in community structure, as there are limited possibilities of stable coexisting assemblages. While strong world-wide convergence in structure caused by ecological interactions appears unlikely, community convergence in itself has been argued to occur (Gillespie 2004; Melville *et al.* 2006), and some have claimed that assembly is deterministic despite evolutionary history in the real world (Emerson & Hewitt 2005).

The antithesis of determinism and convergence is history and specifically how historical events have led to contingency in the evolution of life on Earth (Beatty 1995). Stephen Jay Gould famously postulated that if one were to replay the tape of Life no matter how many times, a single outcome would not be repeated twice (Gould 1989). Gould’s view emphasises that stochasticity of historical events greatly impacts how subsequent events and evolutionary processes unfold (Gould 1989). This means that even if we start from the same beginning we would never obtain the same outcome, as any slight change to a single variable during the replay will be compounded and amplified over time, leading to a different outcome. Although Gould’s thesis is strictly a historical counterfactual and disproving it completely would mean going back in time to ‘replay the tape’, cases of strong convergent evolution might still be informative about when history matters and when it does not.

One example of convergent evolution is the similarity between communities of Greater Antillean Anolis lizards. Anole communities consist of highly similar ecomorphological habitat specialists. While these replicated ecomorphs could have resulted from species dispersing between islands, phylogenetic analyses have shown that they likely arose *in situ* (Losos *et al.* 1998). This indicates that each island consists of independently evolved and convergent communities. However, the case of Anoles may be special in that certain conditions have been met that may be rare to accomplish elsewhere (Losos & Ricklefs 2009): (*i*) Anoles radiated in isolation on islands resulting in reduced competitive and predation pressure, (*ii*) the island system occurs over a restricted area suggesting similar initial conditions, in terms of the vacant ecological niches and habitats, and (*iii*) Anoles are closely related so that the evolution of convergent ecomorphs has happened through conserved or constrained pathways (Powell & Mariscal 2015). Given the particularity of these conditions and the unlikely nature of the repeated occurrence elsewhere, the radiation of Anoles seems to be heavily influenced by a historically contingent series of chance events and conditions.

The order in which historical events take place may greatly impact the structure of communities and specifically those of adaptive radiations such as Anoles. Adaptive radiation has been described as "the proliferation of species from a single ancestor and diversification in many ecologically different forms" (Stroud & Losos 2016). In adaptive radiations the adaptation to distinct unexploited resources or habitat – ecological opportunity – is tightly linked to the accumulation of species. The processes of speciation and niche differentiation that adaptive radiations such as polychromatic spiders on Hawaii undergo to assemble a community may take substantially more time than would assembly through colonisation of an existing set of species (Gillespie 2004). During the radiation of spiders on separate islands, colonisation and filling of unoccupied niches has happened on multiple occasions. This has resulted in polyphyletic clades of spiders that are more distantly related than in situ radiations would have been, as the radiation is prevented from filling the same niche. However, while this changes the phylogenetic structure of the community, the same ecological roles might still be filled. Therefore, along some dimensions of biodiversity community assembly might be deterministic regardless of colonisation or speciation dynamics (Gillespie 2004; Emerson & Hewitt 2005), but might be contingent along others.

Even if the outcome of community assembly were to be deterministic in the end, history might be important in the process of differentiation into multiple niches during adaptive radiations. Imagine now the radiation of Darwin's finches, as they start to diversify across the Galapagos archipelago consisting of many islands, all large enough to sustain a population of finches. Once the ancestral finch arrived on the first island it was met with ecological opportunity in the form of seeds of various sizes and hardness, but proliferation from the ancestral lineage did not happen until the ancestral lineage colonised at least two islands and established allopatric populations (Losos & Ricklefs 2009). Recolonisation of the ancestral island not only depended on stochastic colonisation events, but equally on the partitioning of available resources (Pigot & Tobias 2013). There are two historical questions that arise from this: (*i*) In what order did niche axes get filled (e.g. habitat, resource type, and resource size)? And, (*ii*) when did niche differentiation occur relative to attaining sympatry or coexistence?

The question of the order of niche axis evolution has often been discussed as the progression or stages of adaptive radiation (Losos 2010), but applies more broadly to all co-evolving community members. For instance, Diamond proposed (Diamond 1973, 1986) that niche differentiation of montane New Guinean birds happens in a predictable order. Species first differentiate in habitat type, followed by prey size, and lastly food type. In contrast, Richman and Price (1992) suggested that Old World leaf warblers first differentiate in body size, followed by behaviour and foraging morphology, and lastly habitat usage. Although reconstructing the order in which niche axes diverged is challenging (Losos 2009), these conflicting findings suggest that there may be historical factors that influence the order of niche axis differentiation.

When niches differentiate is potentially as important for community structure as which axes differentiate. The most commonly proposed hypothesis for when differentiation happens is that at secondary contact competition results in differential selection for distinct resources (e.g. seed size, elevation, or habitat use), what is termed character displacement (Lack 1947; Brown & Wilson 1956; Grant & Grant 2006). The key pattern associated with character displacement is that species will appear more differentiated in their ecological niche while in sympatry compared to allopatry. The idea that niches differentiate on contact therefore rests on the assumption that differentiation happens during or after sympatry has been established and not before.

An alternative explanation that would result in the same pattern of higher sympatric differentiation is that niche differentiation may happen prior to establishing sympatry by adaptation to different conditions (Cadena 2007; Losos & Ricklefs 2009).

For instance, species could adapt to different climatic zones or biotic environments. The variation in niches that arose in allopatry will then get sorted against when sympatry is established. Especially when the species attain sympatry relatively rapidly once differentiation has happened, sympatric species might always appear to have higher niche differentiation. By only focusing on contemporary patterns, we thus ignore the order of events. This makes clear that the order of niche differentiation and the establishment of sympatry are important historical events that require further understanding.

Beyond the order of events, the timing of mass extinctions – catastrophic events that have led to the extinction of the majority of life on Earth – have been of major importance to regional biotas and by extension local communities (Jablonski & Sepkoski 1996; Jablonski 2005). For instance, after the KPg mass extinction, once dominant clades such as non-avian dinosaurs ceased to exist, while bivalves recovered (Gould & Calloway 1980) and other clades persisted but have never attained the same diversity that they once held (Jablonski 2002; Barnes *et al.* 2021). As species diversity has to rebuild through speciation, the recovery of ecosystems requires significant amounts of time and is spatially heterogeneous in how fast this occurs (Jablonski 2001). At the same time, mass extinctions leave room for other clades to radiate. Indeed, the rise of mammals after the KPg mass extinction forms one of the classic examples where the extinction of the once incumbent lineages of dinosaurs led to ecological opportunity for mammals (Benton 1983; Rosenzweig & McCord 1991; Stroud & Losos 2016). The limited radiation of clades prior to the extinction of an incumbent ecologically similar clade has often been thought of as the macroevolutionary equivalent of priority effects (Valentine *et al.* 2008). However, the direct link between how competition acting within local communities scales up to affect regional and macroevolutionary dynamics remains understudied.

## History is the timing and order of events

Despite history being a sequence of events through time, the impact of history is frequently evaluated by how static regional properties influence species diversity (Ricklefs & Schluter 1993). Unless experimental approaches are being used the timing and order of events is often not investigated. Ignoring timing and order becomes problematic when we consider that historical events have shaped regional species pools

(Mittelbach & Schemske 2015), determine the outcome of priority effects (Fukami 2015), and facilitate co-adaptation over evolutionary time scales (Weber *et al.* 2017).

A static regional species pool is frequently assumed in community ecological studies and models (MacArthur & Wilson 1967). Briefly, communities are assembled from a regional pool by dispersal and subsequent ecological and environmental filtering. At first sight, this assumption appears sensible as for many kinds of organisms speciation and non-anthropogenically driven extinction are not expected to happen over time scales observable in a human lifetime. Additionally, the species pool should already capture a degree of historical regional effects such as the geographic region, colonisation from other regions, and species accumulation by past *in situ* speciation (Cornell & Harrison 2014). However, although static regional species pools might be reasonable for some scenarios (e.g. when disturbance is frequent and turnover in community composition is fast enough for the species pool to not change between events (Cornell & Harrison 2014), not considering the dynamic nature of species pools, where the timing and order of events matters, could lead to misleading conclusions about the processes that shape communities (Mittelbach & Schemske 2015; Pigot & Etienne 2015).

Species pools are dynamic because of the evolutionary historical processes that can influence community assembly. Under sympatric speciation species would arise within the ancestral community, but under the more common mode of allopatric speciation species arise in geographic isolation, and diversity only increases once newly arisen sister species have attained secondary sympatry (Coyne & Orr 2004; Phillimore *et al.* 2008; Price 2008). The rate at which secondary sympatry is attained is limited by stochastic processes such as dispersal, the attainment of reproductive isolation, and ecological niche differentiation (Weir & Price 2011; Pigot *et al.* 2018). The competitive interactions between sister species that can limit coexistence at local sites, may extend across regions limiting mutual expansion of species into each other’s geographic range (Ricklefs 2008; Pigot & Tobias 2013). These limits to coexistence could in turn scale-up to influence the probability of speciation, because range expansion facilitates new opportunities for geographic isolation (Price 2008; Price *et al.* 2014).

Beyond speciation, it has become increasingly clear that evolution not only alters the regional species pool but can occur rapidly enough to enable species coexistence

(Yamamichi *et al.* 2022), or limit establishment (Urban & De Meester 2009; De Meester *et al.* 2016). In other words, the available species pool that can potentially establish in local communities and their traits can change rapidly over time. That differentiation can happen as a result of competitive interactions spurring differential adaptation (Pastore *et al.* 2021) is perhaps not surprising given the prominence of character displacement in ecological and evolutionary literature (Lack 1947; Brown & Wilson 1956; Stuart & Losos 2013). More interesting is that local adaptation can mediate an evolutionary priority effect – monopolisation – by making it more difficult for maladapted species to invade the same community (Vanoverbeke *et al.* 2016). Therefore, rapid adaptation and the speciation cycle of geographic isolation and secondary sympatry can directly impact local and regional diversity dynamics. This points towards the need to develop a community assembly framework that incorporates the order and timing of historical events.

A source of knowledge that has not been used to its full potential in developing such a framework are phylogenies. Phylogenies have been extensively used in community ecology primarily as proxies ecological and environmental niche distance (Davies 2021). For instance, if the species within the community would show greater phylogenetic pairwise distances than a random sample of species from the regional pool, this was taken as evidence for competitive exclusion dominating community assembly. In contrast, phylogenetic clustering may have indicated environmental filtering, or similar competitive ability among species (Mayfield & Levine 2010). However, such an approach does not take into account the processes that generated the evolutionary history and phylogenetic relationships in the first place.

The timing of speciation events that are captured by phylogenies can be of incredible value to understanding the historical processes that have shaped communities, as the assumption that species arise in allopatry and have to transition to sympatry can be used to understand the timing of community colonisation and trait evolution as will be illustrated in this thesis.

**Outstanding questions**

In the following section I highlight some of the key questions that I think need to be addressed to further our understanding of how evolutionary history and ecological interactions together shape the composition, diversity, and structure of ecological communities.

*How does the evolutionary history of clades shape the richness of ecological communities?*

It is well established that speciation, extinction, and colonisation together should impact communities (Ricklefs 1987, 2004), and that communities are formed by a combination of ecological and historical processes. Yet, the extent to which variation in species richness can be explained by evolutionary history remains unclear because previous studies have either modelled variation richness using proxies for environmental history (e.g. region identity) (Ricklefs & Schluter 1993) or have treated evolutionary history in a relatively simplistic way (e.g. clade age) (Rabosky 2012). Quantifying how the evolutionary history of clades impacts present-day communities thus requires moving beyond static regional and statistical approaches to model the dynamic assembly of communities over time in the context of the historical patterns of species diversification.

*What is the order and timing of niche differentiation in the build-up of coexistence?*

Although quantifying the role of speciation, extinction, and colonisation in shaping communities forms one piece of the puzzle, their impact is modified by ecological interactions. It has become well accepted that ecological interactions and specifically competition can limit the accumulation of species in communities, whereas niche differentiation alleviates competitive pressure and allows coexistence (Pigot & Tobias 2013; Price *et al.* 2014). However, it is unclear whether niche differentiation primarily arises on contact mediated by ecological interactions – character displacement, or by adaptation to variable biotic and abiotic environments in allopatry – ecological sorting. Although both processes have been shown to occur (Cadena 2007; Stuart & Losos 2013), their relative importance, and by extension the order and timing of niche differentiation, for the overall evolution of biodiversity is unclear.

*How do ecological interactions and evolutionary history interact in shaping communities?*

Many ecological models of community assembly ignore macroevolutionary history. Equally, while many mathematical and verbal models exist on how ecological interactions interact with the generation of biodiversity (Simpson 1953; Gavrilets &

Losos 2009; Aristide & Morlon 2019), but few focus on community assembly *per se*. The local community is both the outcome and an integrated part of the regional dynamics that generate and maintain biodiversity and history simultaneously acts in shaping dynamics at both local and regional scales, through the relative timing of colonisation, speciation, extinction, and niche evolution events. Integrating these dynamics in a single model is a key step in understanding the roles of ecology and history in shaping the generation and maintenance of diversity.

## Approach

In this thesis I aim to address the questions outlined above in order to improve our understanding of how the history of species impacts community assembly. In order to accomplish this I use and extend a combination of phylogenetic comparative approaches and develop spatial, phylogenetic simulation models. In **Chapter 2**, I extend a dynamic model of community assembly that integrates the phylogenetic history of species with their spatial distribution. This model is fitted to different passerine clades in order to understand how their unique evolutionary history impacted community assembly, and to what degree evolutionary history predicts community composition and diversity. In **Chapter 3**, I develop a framework based on multistate Markov models to model and estimate when niche differentiation occurs relative to the attainment of sympatry. This framework is specifically applied to the elevational differentiation of montane avian sister species for which I compiled a novel dataset. In **Chapter 4**, I develop a spatial model of species diversification in which local competition for resources limits coexistence. I test how priority effects and its antithesis, invader superiority, influence the dynamics of biodiversity over macroevolutionary timescales. In the final chapter, I synthesise the key findings of these studies and discuss their wider implications.

The approaches that I apply and develop here have certain limitations common for macroecological approaches. First, macroecological approaches to investigate community assembly rely on the accuracy of the underlying data. Although I use state-of-the-art phylogenies and data on species geographic distributions, these still rely on accurate taxonomy, observational records, and the downstream methodologies used to create them. Second, experimental approaches are largely impossible to perform on these temporal and spatial scales. Meaning that the work presented here is largely correlative in nature, and that arguing for causality is difficult. Ideally experiments, such as done for many studies that investigate priority effects (Chappell *et al.* 2022), should supplement my findings here. Third, the scale that I focus on is the species level, and mostly deal with the presence or absence of species instead of their abundances. For instance, this ignores that priority effects rely on the build-up of differential abundances between residents and invaders (Fukami 2015). Yet, a certain phenomenological abstraction is warranted to  remain computationally tractable, establish comparability, and focus on the key biological properties of interest. Fourth, I use range overlap specifically as a proxy of species likely interacting in communities, as well as a proxy of co-occurrence. This has been done extensively in evolutionary ecological studies (Diamond 1973; Pigot & Tobias 2013; Price *et al.* 2014; Freeman 2015; Pigot *et al.* 2018), and makes the comparison between simulation studies **(Chapter 4)** and empirical data **(Chapter 2 & 3)** easier. However, range overlap may not mean that species actually coexist as they might be segregated on a smaller spatial scale (i.e. species are not syntopic). Where warranted I therefore repeat the analysis **(Chapter 2)** on multiple spatial scales, but ideally species inventories should be used in future research.

## Chapter 2:

# Evolutionary history explains community diversity and structure

### Abstract

Ecological communities are assembled over time but the role of evolutionary history in limiting the diversity of species assemblages is poorly understood. Because the formation of new species generally involves a phase of geographic isolation, differences in the build-up of sympatric diversity across space, time and clades may reflect variation in the historical patterns of speciation and thus time available for colonisation. However, quantifying the role of evolutionary history is challenging and thus its potential effects have been neglected compared to models in which ecological limits are the primary constraint on diversity. Here we use a dynamic model of assembly by allopatric speciation, colonisation, and local extinction to test how evolutionary history predicts variation in sympatric diversity across clades of passerine birds. We show that the clade-specific history of speciation strongly impacts the build-up of sympatry over time, and that phylogenetic tree shape can explain a significant proportion of variation in sympatric diversity between clades. Within clades the proportion of species that are sympatric is highest in old, species poor, and phylogenetically balanced clades that radiated early in their lifetime. These historical factors all promote the average age of extant species, providing more time for species to expand their geographic distributions and colonise local communities. We further show that phylogenetic patterns in community structure frequently interpreted as evidence that community assembly is limited by the saturation of ecological niche space can be explained simply by the lag-time to colonisation following speciation. Our results show that the macroevolutionary history of speciation and assembly time is essential in explaining variation in the structure and diversity of biological communities.

### Introduction

The assembly of ecological communities through the speciation of new lineages and their colonisation of local sites is an inherently temporal process. From the succession that ensues following the fall of a canopy tree in a forest, to the ongoing recovery of

Krakatau's island community after the eruption of 1883, to the continued poleward recolonisation of species following the termination of the last glacial period (Pellissier *et al.* 2014), ecological communities bear the imprint of past disturbance and other historical events. However, the role of time and history in explaining variation in the number and combination of species that co-occur in ecological communities remains unclear, especially over macroevolutionary timescales that are beyond the reach of direct observation (Ricklefs 1987).

Because most new species arise in geographic isolation (Coyne & Orr 2004), ultimately the build-up of diversity within ecological communities depends on the expansion of species geographic ranges and attainment of secondary sympatry (Ricklefs & Schluter 1993; Ricklefs 2004; Price *et al.* 2014; Pigot *et al.* 2018; Tobias *et al.* 2020). Previous studies analysing patterns of range overlap among sister species have identified both intrinsic and extrinsic barriers to sympatry, including limited dispersal, reproductive interference and competition for ecological resources. Overcoming these barriers through dispersal, the evolution of reproductive isolation and divergence in ecological niches takes time, with many lineages remaining geographically isolated for millions of years after speciation was initiated (Price 2010; Weir & Price 2011). This suggests that the build-up of sympatric diversity following speciation is often a highly protracted process, occurring at a similar rate to the macroevolutionary diversification of species (Price 2010; Pigot & Tobias 2015). However, testing the extent to which the macroevolutionary history of clades limits the build-up of sympatric diversity is challenging (Mittelbach & Schemske 2015; Pigot & Etienne 2015).

A standard approach for testing the role of evolutionary history in community assembly is to compare local species richness across distinct geographic regions with different geological histories (Fjeldså *et al.* 1999; Graham *et al.* 2006; Pellissier *et al.* 2014). If local richness is strongly controlled by climatically determined limits to coexistence rather than history of past diversification within a region, then communities occurring under similar climatic conditions are expected to converge to a similar level of diversity despite the different geological histories of the regions within which they occur. Studies employing this approach have generally found that while spatial variation in species richness is strongly correlated with the local abiotic environment, substantial residual differences in diversity among regions remain unexplained (Ricklefs & Latham

1993). This residual variation, often dubbed ‘anomaly zones’, have been explained by the unique history of geological events that have impacted the diversification of species and the connectivity of regions, leading to differences in the number of species available to colonise local communities (Ricklefs *et al.* 2006; Ricklefs & He 2016). However, because the actual evolutionary history of clades that constitute these communities is not explicitly considered and because history is treated as a factor that generated statistical noise or anomalies rather than pattern, the role of time since speciation in explaining differences in the build-up of sympatric diversity between regions remains unclear.

An alternative approach that more directly addresses the role of time in community assembly takes a phylogenetic perspective. Studies using phylogenetic reconstructions of when clades colonised different regions, have found that regions that were colonised earlier support more speciose communities, presumably because of the greater time available for speciation and dispersal (Stephens & Wiens 2003; Wiens *et al.* 2011; Kozak & Wiens 2012; Miller *et al.* 2018). However, other studies have questioned this interpretation, showing that the proportion of species in a clade that are found in sympatry is strongly predicted by phylogenetic metrics associated with equilibrium models of diversity. In particular, clades which show stronger slowdowns in diversification rate over time, a potential signal of niche filling, have higher sympatric diversity than clades with a more constant or accelerating rate of diversification. Here, the interpretation is that rather than increasing continuously over time, community richness is capped by an ecological limit and as this limit is reached further speciation is inhibited. In addition, analysis of the phylogenetic branching times among species within individual communities reveal a slowdown in the rate of branching over time, which has been interpreted as evidence that the progressive filling of ecological niche space inhibits colonisation and the build-up of sympatric diversity. While these studies thus variously appear to provide support for both the role of time and ecological limits in regulating sympatric diversity, disentangling these effects is challenging because they rely on statistical correlations between sympatric diversity and phylogenetic metrics rather than a process-based model of how communities are actually assembled over time.

Here, we address this shortfall and provide a process-based framework to test the role of time in explaining the build-up of sympatric diversity within clades, i.e. the proportion of species from a clade that overlap in a locality. Because sympatric richness is constrained by the total diversity of a clade, we focus on testing how macroevolutionary history explains differences across clades in the maximum proportion of species that occur in sympatry at any single location. We focus on 25 family-level clades of oscine and suboscine passerine birds. These groups are ideal for our analysis because they differ widely in both total richness and the maximum number of species that exist in sympatry and because comprehensive phylogenetic and geographic data is available to reliably calculate sympatric diversity and the evolutionary history of each clade (BirdLife International and Handbook of the Birds of the World 2020). Our analysis consists of the following steps. First, we used geographic range maps to identify the locality with the highest number of sympatric species across the distribution of each clade. Second, using the identity of the sympatric species and the reconstructed divergence times of lineages within each clade we applied DAMOCLES (Pigot & Etienne 2015), a dynamic model of community assembly, to estimate the rates of colonisation and local extinction leading to present day patterns of sympatry. Our model assumes that all clades are governed by identical rates of colonisation (and local extinction) and thus differences in the proportion of species in sympatry across clades arise solely due to differences in their history of diversification and the time available for species to colonise local communities (Figure 2.1). Third, we assess the extent to which this model can explain differences in observed proportional sympatry across clades by using the empirically inferred rates to simulate the build-up of sympatric diversity within each clade over time. We compare explanatory power to that of a null model in which the probability of species being in sympatry is independent of the evolutionary history of a clade and is simply determined by the relative rates of colonisation and local extinction. Specifically, the null model assumes instantaneous colonisation of the community, meaning that the ratio between colonisation and extinction rate determines how many species will be present independently of how long they have had to colonise the community. Finally, to help understand the mixed results of previous studies we perform two additional analyses. For both our simulated and empirical datasets, we compare how the maximum proportion of species in a clade that are sympatric correlates with various phylogenetic properties: (*i*) clade richness, (*ii*) phylogenetic imbalance, (*iii*) clade age, (*iv*) $\rho$ – a measure of increases or decreases in diversification rate through time (Pigot *et al.* 2010; Etienne & Rosindell 2012), and (v) the mean terminal branch length – i.e. the average age of each species within the clade. We also use our simulations to test whether slowdowns in branching times among sympatric species, a pattern that has previously been interpreted as evidence of ecological limits and niche filling, can arise purely due to the effects of time for colonisation. Together, our analyses therefore aim to address the role of evolutionary history and in particular time for colonisation in explaining contemporary patterns of biodiversity.

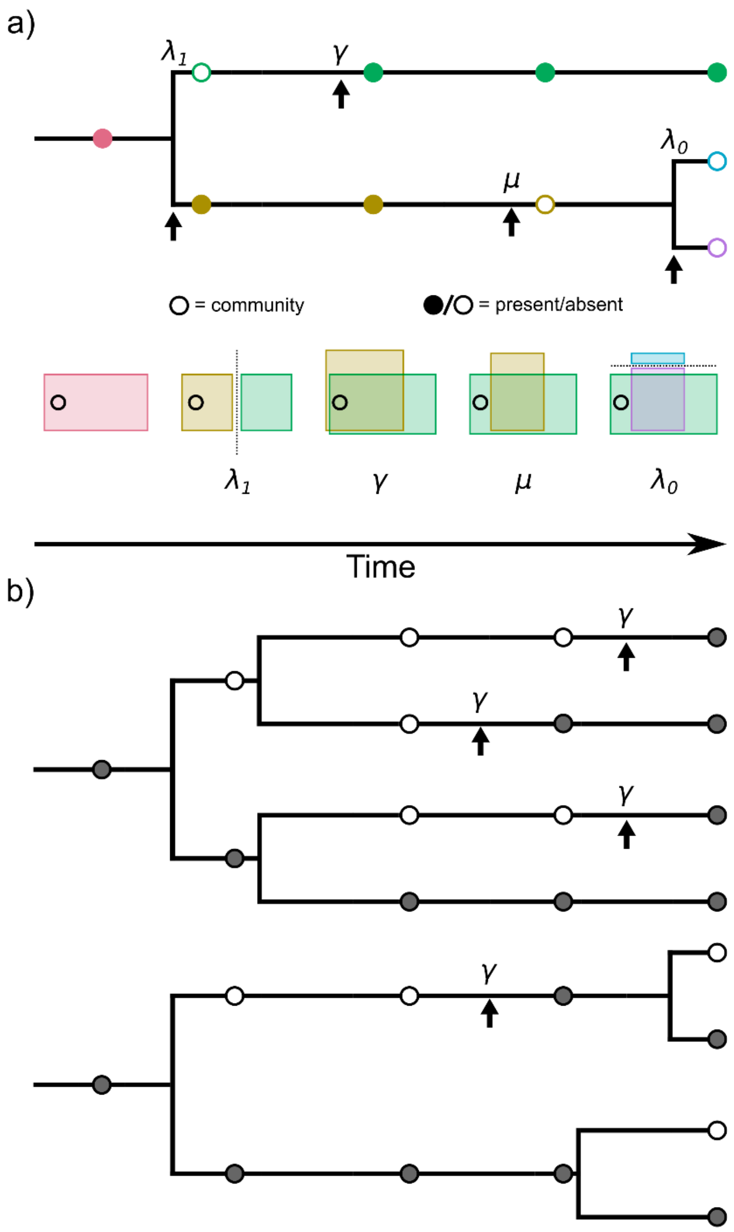

**Figure 2.1** Visualisation of the phylogenetic assembly of communities. a) a conceptualisation of the link between allopatric speciation, range expansion and community diversity. Upward-pointing arrows show timing of events. When speciation occurs by ancestral ranges being divided into two, at maximum one species will be present ($\lambda_1$) in the local community (circles). If the ancestor is not present, neither of the descendants will be present locally ($\lambda_0$). Lineages may become locally present by colonising the community ($\gamma$), or may become absent by experiencing local extinction or extirpation ($\mu$). As these dynamics play out over time, the colonisation and local extinction of species might be conceptualised as the expansion and contraction of species' ranges and the attainment or loss of sympatry between the members of a clade. Note that DAMOCLES only models the colonisation and local extinction of species in the local community along the branches of a pre-existing phylogeny. b) two hypothetical phylogenies, each with four species, with the top phylogeny having older species on average and the bottom younger. Filled circles highlight the presence of a lineage in the local community, and arrows indicate colonisation events. For both phylogenies the ancestor is present in the community, but the dynamics of allopatric speciation and colonisation result in a higher degree of sympatric diversity in the tree with older species.

## Materials and Methods

### *Phylogenetic and geographic range data*

We compiled a dataset consisting of oscine and suboscine passerines predominantly endemic to the Americas. These clades were chosen based on their near complete phylogenies and highly detailed spatial data on the geographic distribution of species. The evolutionary relationships between species and divergence times were obtained from two recently published time-calibrated phylogenies containing >95% (oscines) and >98% (suboscines) of described extant species (Barker *et al.* 2015; Harvey *et al.* 2020). Our analysis focused on how the different evolutionary histories of clades impacts sympatric diversity. Consequentially, the two main phylogenies are divided into family level clades (*n* = 25). The use of families provided a sufficient number of clades to analyse variation in patterns of sympatry but also large enough clades to calculate phylogenetic metrics.

Sympatric diversity for each clade was defined as the total number of species of the focal clade that occurred in a single locality. This was determined by using expert delineated range maps (BirdLife International and Handbook of the Birds of the World 2020). We used expert range maps because in contrast to local species inventories which are not sampled systematically, expert range maps provide a comprehensive characterisation of species richness patterns. The phylogenies and range maps are based on different taxonomies and so we aligned these by using the taxonomy provided by the phylogenetic trees and merging or splitting species geographic ranges accordingly. Species that did not have geographical data associated with them ($n = 5$) were pruned from the dataset. To determine levels of sympatric diversity, range maps were extracted onto an equal area grid of 96 km$^2$ resolution, which is the grain size typically used in macroecological analyses to avoid false presences (Rahbek 2005; Jetz & Fine 2012; Pigot *et al.* 2016). However, to ensure our results were not dependent on the particular grain size used, especially in regions of steep environmental and community turnover we repeated our analyses using 24 km$^2$ grid cells. We were interested in explaining variation in the maximum level of sympatry clades have attained and our model for testing this required data on the presence and absence of species from a single site. For each family-level clade, we therefore identified the grid cell with the highest species richness and the identity of the species present in that cell. Note, that the grid cell with the highest richness could vary across clades.

### *Estimating the dynamics of community assembly*

To determine if evolutionary history could explain differences in sympatric richness across clades we apply and modify the Dynamic Assembly Model of Colonisation, Local Extinction and Speciation, 'DAMOCLES' (Pigot & Etienne 2015). DAMOCLES was originally developed as a null model to evaluate phylogenetic patterns for a single local community. DAMOCLES models the assembly of a single community via colonisation ($\gamma$) and local extinction ($\mu$) along the branches of a phylogeny (Figure 2.1). These rates are constant through time and between species, with the composition of the regional pool provided by the lineages in the reconstructed phylogeny that are extant at that time. Thus, the timing of speciation events through which regional pools evolve are not modelled directly but are instead obtained from the reconstructed phylogeny. Lineages that had not left extant descendants are not considered. We assumed that speciation happened in allopatry and that the area occupied by the community, i.e. either 24 or 96 km$^2$, is too small for *in situ* speciation to occur (Coyne & Price 2000; Kisel & Barraclough 2010). This is a reasonable assumption for birds, for which more than 99% of speciation events are estimated to have involved an allopatric phase and where cladogenetic speciation on islands smaller than Madagascar are extremely rare or debatable (Coyne & Price 2000; Phillimore *et al.* 2008). If speciation happened to a species that was absent from the community, both daughter lineages would equally be absent. In contrast, if the species was present in the community, this would result in one daughter lineage being present locally. Together these dynamics played out over time to make up the present day community composition.

The likelihood approach to estimate $\gamma$ and $\mu$ based on presence-absence data in the focal community and phylogenetic relationships was previously developed (Pigot & Etienne 2015), but we modified the likelihood optimisation workflow. Instead of optimising the likelihood for each family-level phylogeny individually, we optimised a single global rate of $\gamma$ and $\mu$ across all clades under which the cumulative likelihood is maximised. By estimating a single global rate of $\gamma$ and $\mu$, differences in the expected proportion of species that were sympatric across clades in the model arose entirely from differences in their phylogenetic histories. We evaluated a scenario where (*i*) both $\gamma$ and $\mu$ were estimated, and (*ii*) in which only $\gamma$ was estimated thus assuming no local extinction. Model selection was performed by comparing AIC.

### *Simulating the build-up of sympatric diversity*

We tested model adequacy by simulating community assembly forward in time along the branches of each individual phylogeny according to the estimated $\gamma$ and $\mu$. Simulations were implemented via a Gillespie algorithm (Gillespie 1977). Under this algorithm the transition between state 0 (locally absent) and state 1 (locally present) was modelled according to the incidence of colonisation (0->1) and local extinction (1->0) events starting from the root of the tree at $t = 0$ until the present. The model's spatial structure resembled a mainland-island model, where the focal species was either present locally (state 1) or only present at the regional metacommunity level (state 0). The root state of 0 and 1 was randomly assigned with equal probability, and the waiting time till the next event ($\delta$) was drawn from an exponential distribution with a mean equal to the sum of all per-lineage rates. At time $t + \delta$, either a colonisation or extinction event occurred to a randomly drawn lineage with a probability equal to the sum of the respective per-lineage colonisation and local extinction rates. The simulation was repeated a thousand times per clade, resulting in a presence-absence table for the species within each clade. The 95% confidence interval (95% CI) of the predicted proportion of sympatric species was subsequently compared to the empirical proportion of species present in the grid cell with the highest richness. We primarily focus on the proportion of species that are sympatric, but show results for absolute richness as well (Figure S2.1a, S2.3, S2.4).

We compared the ability of DAMOCLES to predict patterns of sympatry to a non-historical null model in which all species in a clade had an equal chance of being present in the focal community and where sympatric richness was thus not influenced by the evolutionary history of speciation. Specifically, we fitted DAMOCLES to the empirical data but instead of estimating both $\gamma$ and $\mu$, we fixed $\gamma$ to a very high rate ($\gamma = 1000$) and freely estimated $\mu$. This resulted in species being able to colonise the community almost immediately once they originate, thus removing the lag-time to colonisation through which evolutionary history is expected to structure patterns of sympatry. Under this model, all species in a clade could theoretically occur in the focal community, but non-zero local extinction will result in lower sympatric richness. Indeed, the ratio between $\gamma$ and $\mu$ determined the proportion of species that would be present in the focal community, and $\mu$ is expected to be estimated at a rate that leads to a similar proportion of sympatric species as is actually observed. Because local extinctions occurred with an equal probability across species, this model thus converges on the standard 'random-draw' model of the community assembly in which species presence and absence is randomly shuffled across the tips of the phylogeny. We evaluated if the model where $\gamma$ was estimated, and thus evolutionary history incorporated, was a better predictor of the proportion of sympatric species than this non-historical model by comparing the proportion of clades where observed sympatric richness falls within the 95% CI of expected values for each model.

### *Predictors of sympatric diversity and phylogenetic structure*

For each of the family-level phylogenies, we quantified the following metrics: (*i*) the crown age, (*ii*) Colless' index of imbalance standardised to the 'proportional to distinguishable arrangements' model in order to be independent of tree size and richness (Mooers & Heard 1997; Bortolussi *et al.* 2006), (*iii*) relative temporal shifts in diversification (speciation – extinction) rate between the first and second half of the phylogeny according to the $\rho$ metric (Pigot *et al.* 2010; Etienne & Rosindell 2012), and (*iv*) the mean terminal branch length (*mbl*) used as a measure of the average age of extant species. We only considered families with more than five species as calculating phylogenetic properties for smaller trees become less informative. For instance, $\rho$ would only be able to obtain a limited set of values as diversification either happens in the first half ($\rho$ = -1) or second half ($\rho$ = 1*).*

To investigate how these phylogenetic properties correlated with sympatric diversity, and if these predictors matched between simulations under DAMOCLES and the empirical data we performed a series of generalised linear models. We assume respectively binomial and Poisson error distributions with a logistic link function when proportions and absolute counts of locally present species are the response variable. Proportions were weighted for total clade species richness (Douma & Weedon 2019). The following predictor variables were included prior to model selection: clade age, mean terminal branch length, $\rho$*,* phylogenetic imbalance, and log-transformed clade species richness. The aim was to understand how clade-specific evolutionary histories represented by phylogenies influence sympatric diversity, and if these same properties are predicted by DAMOCLES.

As a final part of our study we investigate how assembly over time impacts phylogenetic structure. For each clade we compared phylogenetic metrics calculated at the level of family and at the level of the focal community (i.e. grid cell of maximum sympatric richness) by pruning the family-level phylogeny to only those species that are present. Specifically, we calculate (*i*) Colless' index, (*ii*) $\rho$ , and (*iii*) the *mbl* for these community-phylogenies. The aim of this analysis was to test whether phylogenetic properties of sympatric communities previously interpreted as evidence of ecological limits constraining diversity can also be explained by our model accounting for macroevolutionary history but in which ecological limits are absent.

### *Workflow summary*

The workflow of our study can be summarised as follows: first, an empirical dataset of family-level phylogenies and communities that showed the highest sympatric diversity per clade were compiled. Second, DAMOCLES was fitted to the empirical data to estimate rates of community colonisation and local extinction across all clades. Third, these parameter estimates were used to simulate communities along the branches of the same empirical phylogenies. The proportion of sympatric species is compared between the simulated and empirical communities to assess model adequacy. Fourth, the explanatory power of the model is further assessed by comparing the historic null model to a null model without evolutionary history. Fifth, we quantify the shape of the phylogenies and test how this correlates with sympatric diversity for both empirical and simulated communities. Finally, we compare how these metrics of tree shape change from the complete phylogeny to only contain those species that are locally present for both the empirical and simulated communities.

## Results

### *Model estimates and predictions*

Our final dataset consisted of 7 oscine and 18 suboscine clades that ranged from 6 to 354 species in size with the maximum proportion of locally present species ranging from 0.155 to 1. We found that for these clades the estimated rates of colonisation ($\gamma$ = 0.122 Myr$^{-1}$) and local extinction ($\mu$ = 0.122 Myr$^{-1}$) were remarkably slow. This was equally the case when we only estimated colonisation ($\gamma$ = 0.075 Myr$^{-1}$). The scenario where only colonisation is estimated (AIC = -2494.75) provides a substantially better fit (ΔAIC = 52.339) compared to when local extinction is estimated (AIC = -2442.41). The colonisation-only scenario was also favoured when we focused on a smaller spatial grain size (24 vs. 96 km$^2$) at which communities were delineated (AIC$_\gamma$ = -2319.93 and AIC$_{\gamma\mu}$ = -2283.75). An even slower rate of colonisation ($\gamma$ = 0.060 Myr$^{-1}$) was estimated when communities were constructed from the 24 km$^2$ grid cells.

The model adequacy analysis showed that the estimated colonisation rate resulted in good predictions of the empirical proportions of sympatric species for the different clades well. For 22 out of 25 clades the observed proportions fell within the 95% CI of the proportions predicted by the Gillespie algorithm simulations. The maximum proportion of sympatric species was underestimated for Onychorhynchidae and Dendrocolaptidae, and overestimated for Rhinocryptidae (Figure 2.2). At the 24 km$^2$ grain size the maximum proportion of sympatric species was underestimated for Dendrocolaptidae and Parulidae and overestimated for Rhinocryptidae (Figure S2.1). This indicated that based on the phylogenetic history of a clade and a single colonisation parameter we could accurately estimate the maximum proportion of species that were sympatric within a clade and the variation in levels of sympatry across avian families.

We find that a non-historical null model explains variation in sympatry less well, with respectively 15 out of 25 at the 96 km$^2$ scale and 16 out of 25 clades at the 24 km$^2$

scale having observed levels of sympatry within the 95% CI of the null model, including the three clades that fell outside the 95% CI of the historical model in which $\gamma$ is estimated to be low (Figure 2.2, S2.1). This indicates that the simulations under DAMOCLES capture the empirical proportions well, and better than the null model, but we emphasise that predicting the proportion of sympatric diversity should not be overinterpreted and primarily be seen as a model adequacy check.

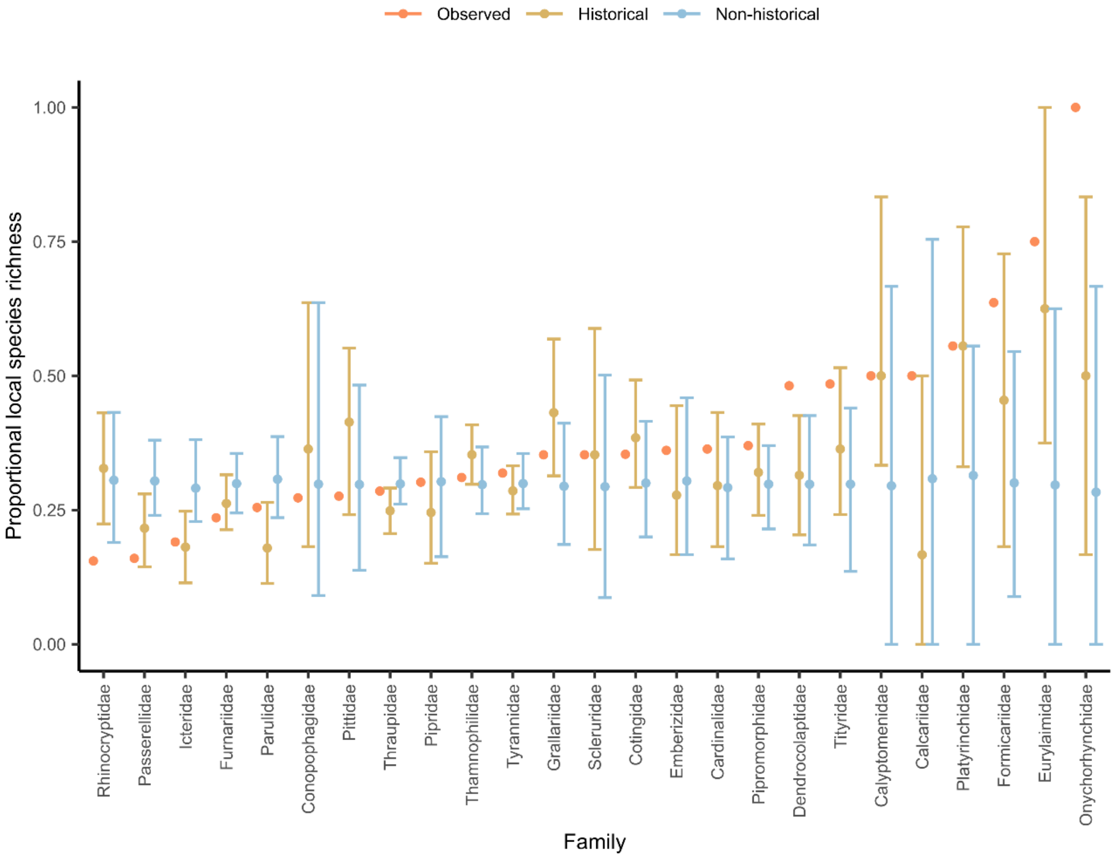

**Figure 2.2** Observed and predicted proportional richness of passerine clades. The empirical (orange) data points show the maximum proportional richness of the clades across 96 $km^2$ grid cells. Clades are ordered along the x-axis from low to high empirical maximum proportional richness. Predictions for the historical model under the colonisation rate recovered by DAMOCLES (yellow) and the non-historical model where colonisation rates are very high (blue) are shown. Bars represent the 95% confidence intervals of the proportional richness of the community recovered under 1000 simulations. For the historical model 22 out of 25 empirical proportion fall within the 95%CI, whereas 15 out of 25 fall within the CI's of the non-historical null model.

### *The predictors of the sympatric diversity across clades*

The minimum adequate model for both the empirical and simulated data was one where the mean terminal branch length, *mbl*, had a significant positive effect on the maximum proportion of locally co-occurring species across the clades (Figure 2.3b). We note that when we removed *mbl* from the model other phylogenetic metrics show a significant relationship with the proportion of sympatric diversity, indicating that the same information is captured by a combination of other metrics. Clade age showed a positive relationship, while clade species richness had a negative effect on the proportion of sympatric species. While there is no effect of phylogenetic imbalance in the simulated data, clades with more balanced phylogenies showed higher observed proportional sympatric diversity. In contrast, clades that show slowdowns in diversification rate (i.e. $\rho < 0$) only show a significantly higher proportion of sympatric diversity in the simulated data and not in the empirical data. The strong positive effect of *mbl* on sympatric diversity is again consistent across spatial grains used to define sympatry (Figure S2.3b). Notably, the intercept and positive effect of *mbl* on the proportion of sympatric species are comparable between the simulations and the empirical model fit. Although the variance explained by *mbl* for the simulated data (pseudo-$R^2$ = 0.824) is markedly higher than for the empirical data (pseudo-$R^2$ = 0.304) our results suggest a potential causal relationship between the evolutionary history of a clade and the time to colonisation that this provides, in predicting the number of sympatric species.

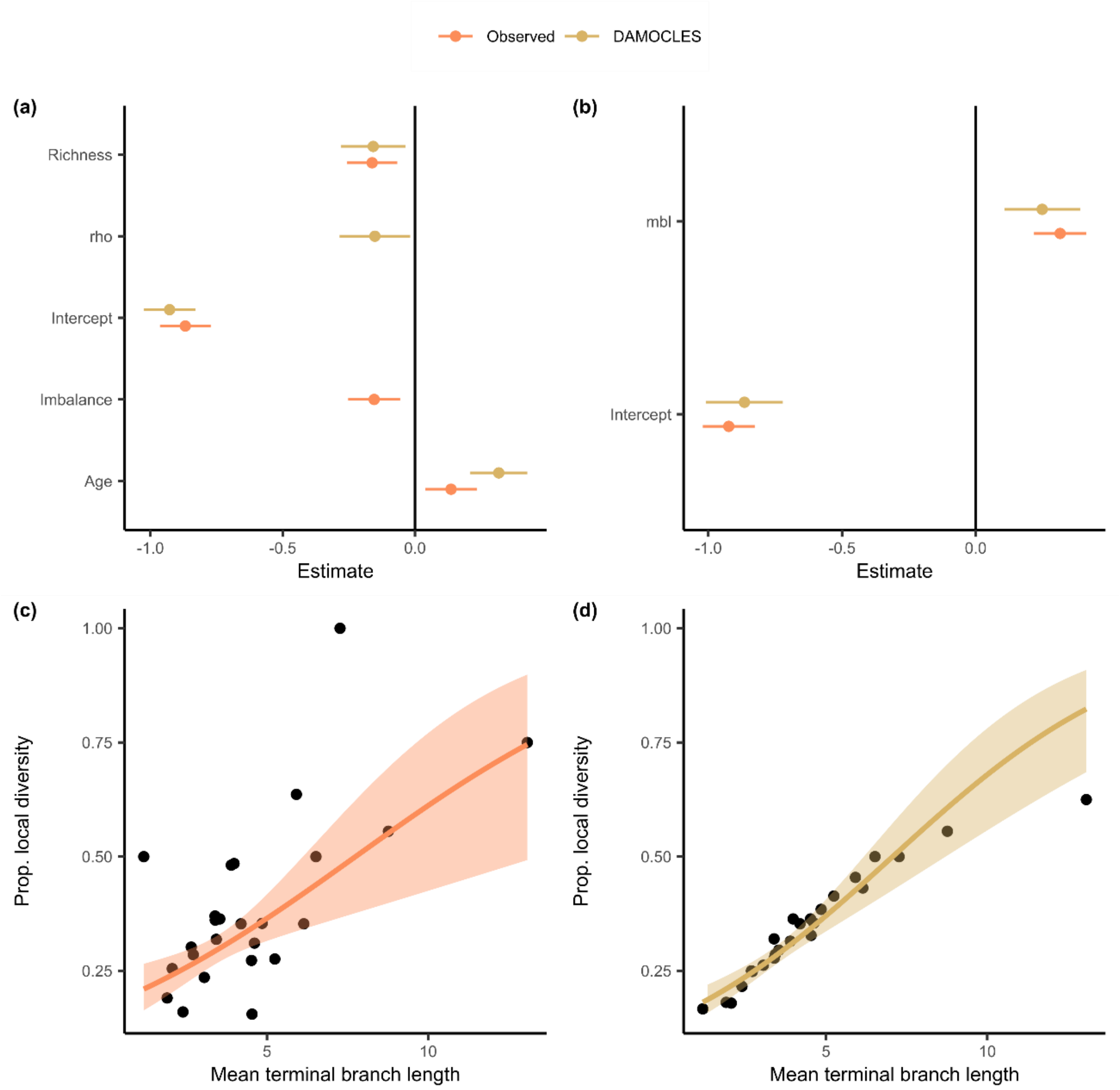

**Figure 2.2** Relationship between evolutionary history and sympatric diversity. Colours denote the empirical relationships for all clades (orange) and relationships simulated under DAMOCLES are shown in yellow. (a) Minimum adequate models (MAMs) for the explanatory variables where mean terminal branch length had not been added are shown. Non-significant variables are not shown. (b) MAMs for models including mean terminal branch length (mbl). GLM Input data was scaled and mean-centred for visualisation, and bars represent 95%CI's. Predicted relationship between mbl and the maximum proportion of species in sympatry for the (c) empirical and (d) simulated data highlighted by the coloured lines. Shaded areas indicate 95% CIs, and black dots represent respectively the (c) empirical data and (d) data simulated under the recovered parameter values.

### *The relationship between clade and community level phylogenetic metrics*

We found that phylogenetic trees that had been pruned to only consist of the sympatric species, community-level phylogenies, show distinct, predictable patterns compared to the family-level phylogeny. For instance, community-level phylogenies tended to show a decrease in diversification rate with time (i.e. $\rho < 0$), and species were older on average

(Figure 2.4a, b, e, f). In contrast, phylogenetic imbalance did not show a clear trend (Figure 2.4c, d). These results were consistent between empirical and simulated data. While especially slowdowns in local communities have been associated with ecological limits, our results indicated that they could equally result from the delay in colonisation of the community after allopatric speciation.

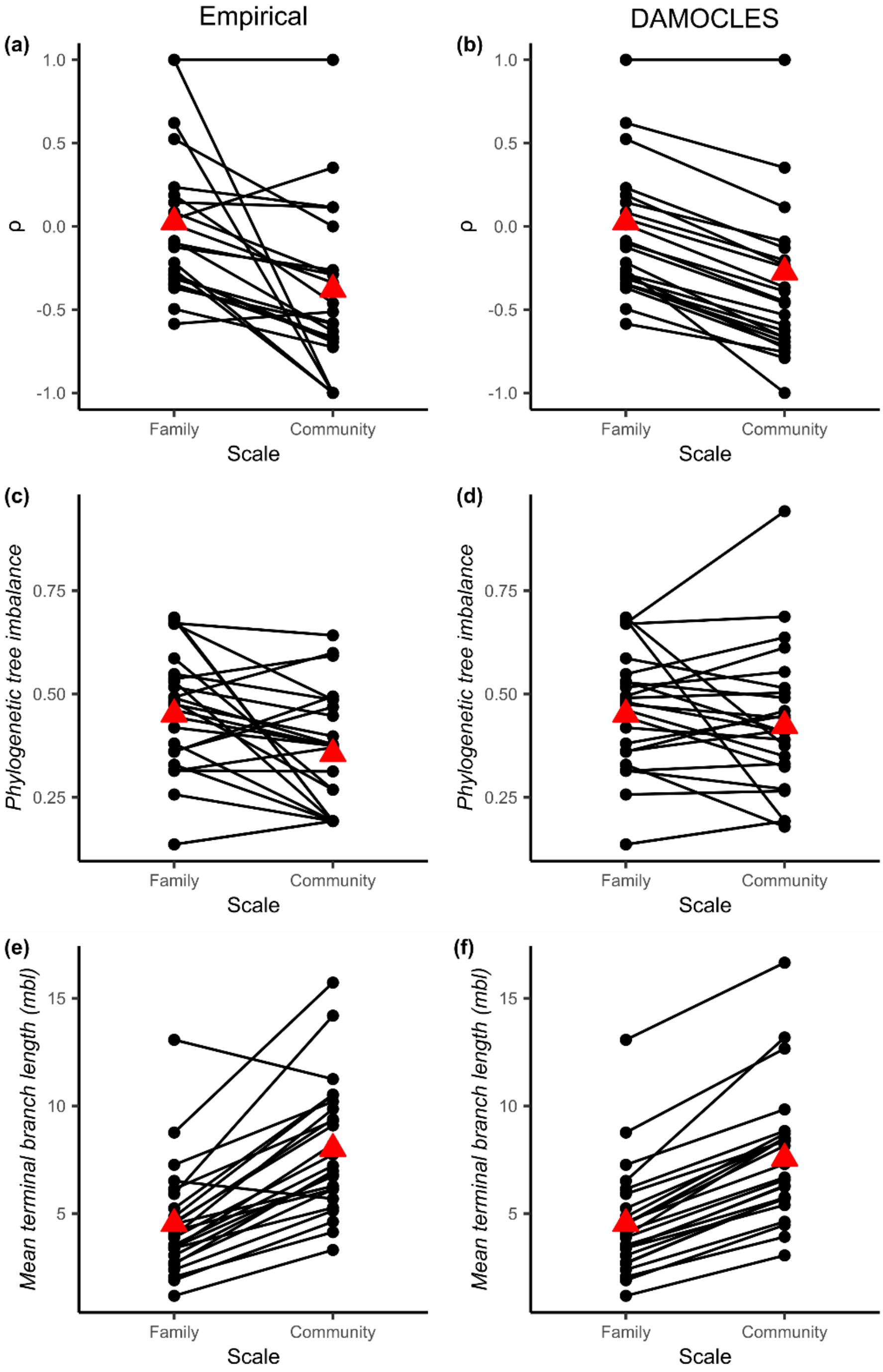

**Figure 2.3** Community phylogenetic structure for the empirical and simulated data sets. Three metrics are shown and compared between the entire family-level phylogeny and the phylogeny constructed from only those species that are present in the local community (i.e. grid cell of maximum richness) for each family. Column 1 shows the empirical patterns, whereas column 2 shows the patterns as found under the

historical DAMOCLES model where colonisation rate was estimated. (a, b) $\rho$ or delta diversification rate shows the change in diversification rate over time. Negative (positive) values show decreases (increases) in the net diversification rate. (c, d) Phylogenetic imbalance as measured by Colless' index and normalised according to the PDA model. Higher values indicate increasingly unbalanced phylogenetic trees where most diversity is concentrated in few lineages. (e, f) mean terminal branch length or the average age of the extant lineages.

## Discussion

The evolutionary history of speciation, extinction and colonisation has been argued to be of fundamental importance to local communities (Ricklefs 1987). However, a mechanistic perspective of how communities are assembled via allopatric speciation and secondary sympatry has not been incorporated into the study of sympatric diversity patterns (Mittelbach & Schemske 2015). Here, by expanding upon a macroevolutionary model of community assembly where the dynamics of diversification, colonisation and local extinction each play a role, we show that evolutionary history and the time available for colonisation are of fundamental importance in explaining variation in levels of sympatry across clades. In particular, we show that a model incorporating only phylogenetic history and assuming a single rate of colonisation across a set of avian families with radically different ecologies, can explain substantial variation in the proportion of species that are sympatric within any clade. We show that this historical model outperforms a null model in which evolutionary history is ignored. The proportion of sympatric diversity and the phylogenetic properties that explain it are largely consistent between simulations of our model and the empirical data. Both analyses show that the strongest predictor of proportional sympatric diversity is the mean terminal branch length of a clade, as this indicates the time available for species to colonise the local community following speciation. Lastly, we show that community-phylogenetic patterns previously interpreted as evidence that sympatric diversity is regulated by ecological limits (e.g. slowdowns in diversification rate within a community phylogeny), can equally be explained by the lag-time to colonise the community post-speciation.

Earlier studies seeking to explain variation in sympatric diversity have focused on the role of time for speciation, where it is argued that the earlier colonisation of a region provides more time for speciation events to occur (Stephens & Wiens 2003; Hutter *et al.* 2013). However, these studies did not capture evolutionary history beyond the initial colonisation of a region. This means that for a given clade age or time of initial colonisation, differences in the historical dynamics of diversification and when speciation events happen, does not have any effect on the local diversity of the community. However, as we show here, when speciation happened is vital for determining sympatric species diversity, as the older the species are, the more time they have had to colonise the local community after speciation in allopatry. Thus, by not accounting for the finer-grained historical patterns of individual speciation events, the role of time in explaining variation in sympatric diversity may have been underestimated.

Macroecological studies have variously used phylogenetic properties, diversification rates, and diversity measures to infer ecological processes such as competition from biogeographic patterns. For example, Weir (2006) showed that clades of Amazonian birds showing stronger slowdowns in diversification rate over time had higher levels of sympatric diversity, and interpreted this as evidence that niche space within local communities was saturated, inhibiting further range expansions and speciation (Weir 2006). The results of our study reverse this interpretation, showing that clades that have undergone slowdowns in diversification have higher sympatric diversity due to the greater age of extant species and thus time for colonisation. This does not rule out the possibility that ecological limits have caused a slowdown in diversification rate (Rabosky & Hurlbert 2015), but shows that relationships between phylogenetic metrics and sympatric diversity do not provide evidence of ecological limits.

Another pattern where our model results alter previous explanations regards temporal slowdowns in the rate of branching among species present in a community. The appearance of such a slowdown is not simply a result of the well-known artefact of incomplete sampling of a phylogeny (Cusimano & Renner 2010), and has thus been interpreted as evidence that rates of colonisation slow down over time as niches are filled (McPeek 2008; Price *et al.* 2014). However, our results show that the appearance of such a slowdown arises even when rates of colonisation are constant over time. This is because allopatric speciation results in an overdispersed phylogenetic structure of communities (Pigot & Etienne 2015), with fewer closely related lineages co-occurring than expected from random sampling. While it was recognised a decade ago that the appearance of slowdowns in diversification rates could arise because speciation takes time (i.e. protracted speciation (Etienne & Rosindell 2012)), here we show that the appearance of slowdowns in community assembly can arise because colonisation takes time. We refer to this as the principle of protracted colonisation. Conditions that would need to be met for protracted colonisation to have no impact on community phylogenetic metrics is that speciation primarily happens *in situ* so that species do not have to colonise the area from outside, or that *in situ* cladogenetic speciation is absent from the regional community against which the local community is being compared. The process of protracted colonisation should therefore be considered in many macroecological studies that focus on local assemblages that are small but regional assemblages that are large compared to the spatial scale of cladogenetic speciation.

Our estimates of the time to sympatry for species in our clades is similar with earlier findings for sister pair analyses. For instance, Pigot & Tobias (2013) found that it takes on average 14.52 Myr for sister species of Furnariidae to reach secondary sympatry (Pigot & Tobias 2013). This is remarkably similar to the 13.36 (96 km$^2$) and 16.59 Myr (24 km$^2$) for species to attain sympatry estimated in our analysis (note that Furnariidae are included as one of the families in our analysis). This suggests not only a degree of conservatism across clades in the factors that limit range expansions and community assembly, but also that the rate at which species transition to sympatry is consistent between sister species and more distantly related species. This provides support for the utilisation of sister species in studying diversity dynamics, and may suggest that processes such as dispersal limitation and competition that have been found to regulate the transition rate to sympatry between sister pairs scale to entire clades as well (Pigot *et al.* 2018).

Previously, evidence that time matters for the build-up of diversity has been used as evidence arguing against ecological limits to diversity (Stephens & Wiens 2003; Wiens 2011). This evidence is controversial and has been scrutinised extensively, on the basis of both methodological and conceptual issues (Rabosky 2012; Stadler *et al.* 2014; Rabosky & Benson 2021). Our study supports a key role for time in the build-up of sympatric diversity and shows that this may provide an alternative, and potentially more parsimonious, explanation for phylogenetic patterns previously interpreted as evidence of ecological limits. However, it is important to note that our model does not identify the factors that delay the attainment of sympatry and cause a lag between speciation and colonisation of the community. It is possible that including parameters that quantify the effects of ecological interactions between species or limits to diversity could further improve model explanatory power (see **Chapter 3**). Furthermore, while our analysis focusses on explaining variation in the proportion of species that are sympatric, our model is silent to the causes of variation in clade level richness and the processes regulating diversification rates over time. In other words, variation in evolutionary history between clades that determine sympatric diversity, such as the strength of slowdowns in diversification rate or the degree of phylogenetic imbalance, could be caused by differences in ecological limits or the strength of species interactions (See **Chapter 4**). Therefore, our results do not rule out ecological limits to diversity locally nor regionally, but offer another perspective that will need to be considered before conclusions can be made about ecology's role in regulating species diversity.

Our results show that a simple model based only on the macroevolutionary history of clades enables robust predictions about the variation in diversity and phylogenetic structure of communities. However, our analysis of patterns of sympatric diversity is based on but one inventory of species from each clade, where sympatry is highest. However, many different assemblage configurations can occur by chance, alternative stable states can be facilitated by which species arrives first (i.e. priority effects) (Fukami 2015) (see **Chapter 4**) and levels of sympatry can vary substantially across different parts of a clades distributions. Understanding the causes of these differences in assemblage diversity within clades will be an important next step in determining how sympatric diversity is constrained by ecology and evolutionary history. Furthermore, our stochastic model lacks the ability to make precise predictions about community composition and in particular which species are likely to be present. For example, while our model predicts that the probability of both sister lineages co-occurring locally should increase with the time since they diverged, we cannot predict which lineage will be present at any given time as both are governed by identical colonisation rates. An important extension of our model would therefore be to incorporate key environmental and ecological factors, such as differences in dispersal ability and niche divergence (see **Chapter 3**) , that are expected to influence the likelihood of range expansions and which combinations of species are able to coexist. While the simple models we have employed here provide a powerful approach for isolating the effect of time for colonisation on sympatric diversity, a complete understanding of the role of evolutionary history in community assembly is likely to require more complex models that account for the interactions between species and the feedback between local diversity and the dynamics of species diversification.

## Chapter 3:

# Disentangling the historical routes to community assembly in the global epicentre of biodiversity

### Abstract

The coexistence and turnover of species along elevation gradients makes tropical mountains hotspots of biodiversity. However, understanding the historical processes through which species arising in geographic isolation (allopatry) assemble along the same mountain slope (sympatry) remains a major challenge. Here, we apply continuous-time Markov models to elevational, geographical and phylogenetic data for 166 avian sister pairs to infer the relative frequency of different historical pathways involved in the species build-up on Neotropical mountains. We show that sister species have assembled through a mix of processes. Ecological sorting whereby species diverge in elevations in allopatry occurs with similar frequency to ecological displacement where divergence occurs upon secondary contact. However, by far the most species reach sympatry without diverging in their elevation. The ability of closely related species to coexist without elevational divergence provides a more direct and faster route to sympatry and may help explain the exceptional richness of tropical mountains.

### Introduction

Explaining the combination and diversity of species that co-occur within communities remains a major challenge in ecology. This is in part because the patterns of spatial overlap observed at the present depend not only on current ecological interactions between species, but also on historical processes that play out over much longer time-frames and that are beyond the reach of direct observation or experimental manipulation (Weber *et al.* 2017). These historical processes include speciation, niche evolution, dispersal, and range expansions (Mittelbach & Schemske 2015), with differences in the dynamics of these processes and the ecological factors controlling them, underlying different theoretical models for how communities are assembled.

One of the main models for how communities assemble is based on the idea that new species arising in spatial isolation (i.e. allopatry) diverge in their ecological niche, and only those that happen to diverge sufficiently to minimise competition are able to co-occur when they come back into secondary contact (Pfennig & Pfennig 2010; Stuart & Losos 2013). According to this model, community assembly largely involves the 'ecological sorting' of pre-existing variation arising due to geographically variable selection pressures. An alternative to the ecological sorting model, proposes that niche differences between co-occurring species arise upon secondary contact, with competition between species driving divergent selection and a displacement of their ecological niches (Brown & Wilson 1956). As with ecological sorting, this 'ecological displacement' (termed 'character displacement' when considering heritable traits) model assumes that niche similarity limits co-occurrence, but differs in its predictions of when and why niche differences evolve. A final possibility, is that species may re-assemble into communities whilst retaining their ancestral niche. This 'niche conservatism' model (Cadena *et al.* 2011) is expected to predominate if ecological niche overlap is not limiting, either because of other constraints on co-occurrence (e.g. dispersal limitation) or because species have diverged along alternative niche dimensions (Pigot *et al.* 2018).

A classic system and spatial parallel for studying these historical processes concerns the distribution of vertebrates on tropical mountain slopes. Tropical mountains are renowned for their exceptional diversity. For instance, in the tropical Andes over 800 species of birds can be found living on a single mountain slope (Walker *et al.* 2006). Since most speciation events involve the geographic isolation of populations on different mountains (i.e. allopatry)(Price 2008; Cadena & Céspedes 2020; Linck *et al.* 2020), the main problem is to understand how these species subsequently assemble on the same mountain slope (i.e. sympatry) and partition ecological niche space. In this case, sympatry may involve species co-occurring at the same elevation. However, elevation can also be regarded as a key niche axis along which species can diverge and thus coexist at the scale of the entire mountain slope. Indeed, many species have very narrow elevation distributions (e.g. a few hundred metres in vertical distance) and replace one another across the gradient (Diamond 1973; Terborgh & Weske 1975). Previous studies have variously provided evidence that conservatism, sorting, and displacement of elevational ranges may individually be involved in shaping these patterns of range overlap and turnover along mountain slopes, but progress in disentangling their relative contributions has been limited.

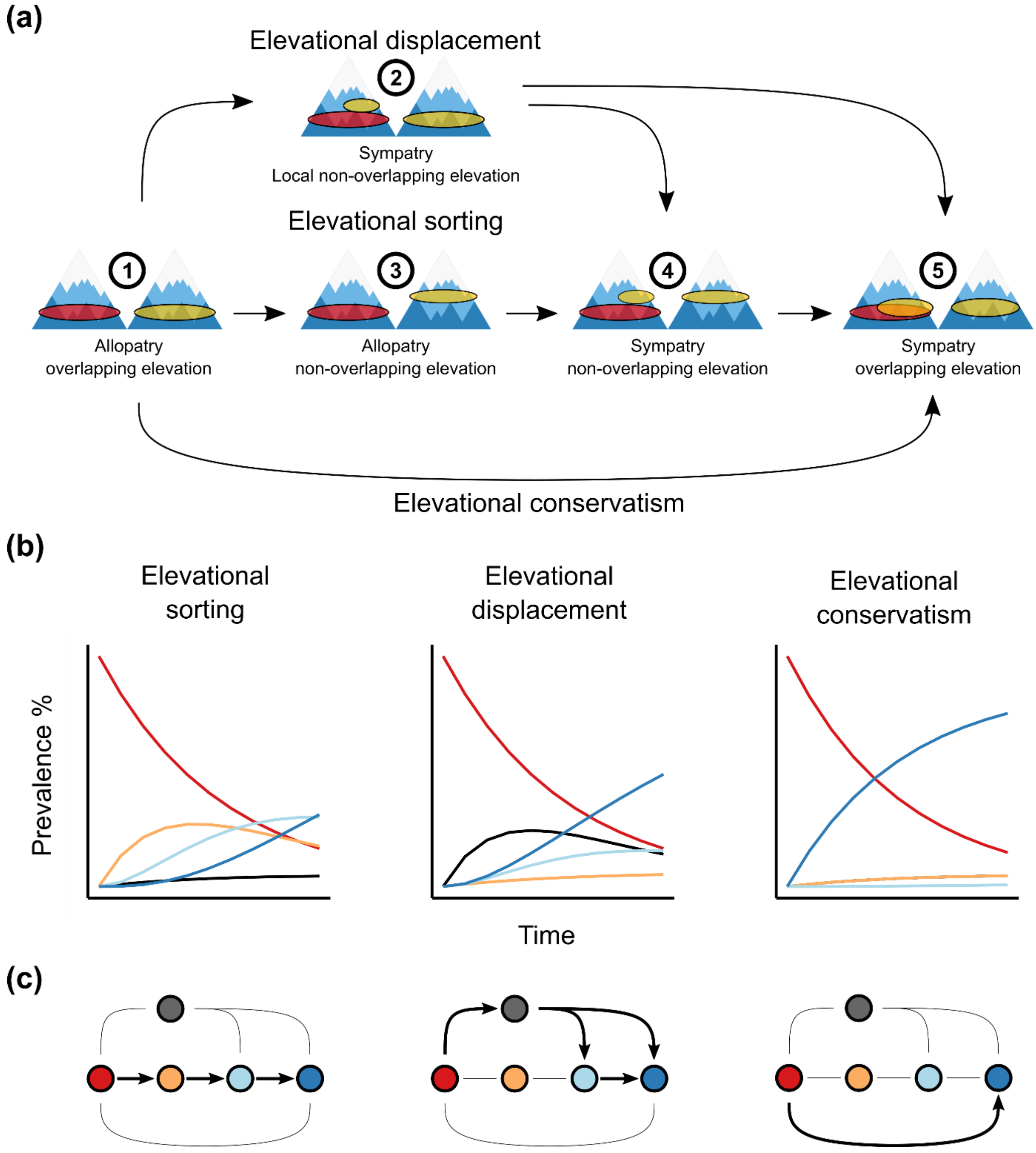

**Figure 3.1** Hypothetical trajectories towards sympatry in montane sister species. a) All possible transitions in our models with their respective geographical and elevational context. (1) Species originate in allopatry

and initially share the same elevational range. Subsequently, pairs might either stay in allopatry, but diverge in elevational range (3), attain partial elevational differentiation only in sympatry but retain overlap in allopatry (2), transition to sympatry but with differentiated elevational ranges (4), or transition to sympatry and co-occurrence (5). b) The prevalence of the five states through time according to the three hypothesised trajectories: elevational sorting (ES), elevational displacement (ED) and elevational conservatism (EC). Colours in b) and c) map on the states as shown in a), and columns in b) correspond to c). These hypotheses are based on simulations in which the respective pathways are dominant.

One problem is that different assembly models can lead to the same present-day pattern. In particular, according to the elevational conservatism (EC) model, species living on the same mountain slope have overlapping elevation ranges because they retain the adaptations to specific environmental conditions inherited from their ancestor (Cadena *et al.* 2011) (Figure 1a). However, while some studies have argued that elevational conservatism is a pervasive process (Linck *et al.* 2021), the same pattern could also arise under the elevational displacement (ED) model. Under ED, competition on secondary contact first forces species to occupy different elevations, but as species diverge in, e.g., resource or microhabitat use they may subsequently expand their elevation ranges and overlap along the gradient (Figure 1a). The ED model has been proposed to be the dominant process explaining the build-up of species within elevation zones on tropical mountains (Diamond 1973; Freeman 2015).

A similar challenge exists when trying to discriminate elevational displacement from elevational sorting (ES). Both these models predict that species living on the same mountain slope should have non-overlapping elevation ranges, at least prior to any subsequent expansion in elevation range. Thus, discriminating between these scenarios depends critically on inferences about whether elevational divergence precedes (i.e. ES) or is coincident with (i.e. ED) the attainment of secondary contact (Figure 1a). Studies attempting to address this issue have variously used phylogenetic information to infer the relative timing of elevational divergence and secondary sympatry or have compared elevation divergence between sister species in zones of sympatry to places where they remain allopatric (Freeman 2015; Cadena & Céspedes 2020). However, while such tests can potentially detect evidence of whether a particular process operates or not, critically they do not reveal how frequently this process occurs and thus its relative contribution to the build-up of sympatric diversity and elevational turnover (Anderson & Weir 2021). For example, there is no reason to think that only one of these processes is determining the assembly of the remarkable bird diversity within the Andes. Progress in understanding community assembly, thus requires new approaches that can reliably infer the relative frequencies of different historical processes underlying current patterns of species distributions.

Here, we investigate the relative frequency of elevational displacement, sorting, and conservatism and how they contribute to the co-occurrence of passerine birds across elevation gradients in the Neotropics. We first constructed a new dataset consisting of the divergence time, geographical and elevational distribution of $n$ = 166 sister species. We then apply a novel modelling approach that builds on previous studies examining the transition to sympatry using continuous-time Markov models (Pigot *et al.* 2018), but extend this framework by considering the multiple routes through which species can attain sympatry via the evolution of elevational ranges. Focussing on avian sister species, where we can confidently assume that speciation involves the geographic isolation of populations (Phillimore *et al.* 2008; Price 2008), allows us to use information on the current age and state (e.g. allopatric or sympatric, and overlapping in elevation or not) to model the historical pathways through which patterns of geographic and elevational range overlap arise. Using this approach, we address three main objectives. First, what is relative importance of elevational sorting, displacement and conservatism in build-up of sympatry among Neotropical montane sister species? Second, what is the relative importance of elevational sorting and displacement in generating turnover between sister species across elevation gradients and how does co-occurrence (i.e. range overlap) at the same elevation arise? Third, can our framework accurately and precisely infer the rate at which species pairs pass through these different historical routes?

## Material and methods

### *Elevational and geographic data*

We compiled a dataset consisting of avian sister species occurring in the tropical mountain ranges of the Neotropics. Sister species and their respective divergence times were extracted from two recently published phylogenies covering respectively >95% and >98% of the New World oscines and suboscines (Barker *et al.* 2015; Harvey *et al.* 2020). We only retained sister pairs that met the following conditions: (1) At least one of the species occupies montane habitat, defined as areas >500m above sea-level (Freeman 2015). (2) Both species occupy predominantly humid environments such that species pairs could realistically live on the same mountain slope and macrohabitat, e.g. we removed species pairs if one sister occupied predominantly arid habitat and not humid forest, assessed with information from field guides. (3) Both species live in the Neotropics, which included the tropical mountain ranges of Central-America. Species that had ranges stretching into North-America were included in the dataset if they were primarily Neotropical. The final dataset consisted of $n = 166$ sister pairs. To test whether our conclusions were robust and to compare with previously published results that have used alternative statistical methods, we also reanalysed a previously published global dataset of montane sister species (Supplementary material, Figure S3.2) (Freeman 2015).

We scored whether each sister pair was allopatric or sympatric and whether they had overlapping or non-overlapping elevational distribution using geographical (Figure S3.3) and elevational range data gathered from a number of sources, including Stotz *et al.* (1996) and regional field guides and surveys (Hilty & Brown 1986; Stotz *et al.* 1996; Ridgely & Greenfield 2001; Hilty 2003; Walker *et al.* 2006; Schulenberg *et al.* 2007; Athanas & Greenfield 2016; Vallely & Dyer 2018). We supplemented this with *Birds of the World (BW)* (Billerman *et al.* 2020) that typically reflects information found in local field guides but incorporates more recent taxonomic changes. We note that, although not primary scientific literature, field guides offer a wealth of expert knowledge on the natural history of birds and are frequently used in studies of bird elevation distributions, e.g. (Quintero & Jetz 2018).

Our method requires treating geographical and elevational overlap as discrete states. We defined species as having overlapping elevation ranges if overlap was ≥20%. This threshold was chosen to avoid classing species which only meet marginally along narrow contact zones as overlapping. To test the robustness of our conclusions, however, we also repeated our analysis using different values (1, 10, and 30% overlap, Figure S3.1). Sympatry was defined as when sister species were present on the same mountain slope, regardless of whether this overlap was widespread (i.e. thousands of kms) (Figure S3.3f, i) or minimal (i.e. a few kms) (Figure S3.3g, h). We did not use metrics of absolute or proportional range overlap to define sympatry because this is unsuitable for montane systems where one species can have a very small geographic range (e.g. Figure S3.3b, e, g, h), or where species might occur above one another in sympatry (Figure S3.3d North West Colombia). In practice, defining sympatry was unambiguous as allopatric pairs typically occurred on different mountain summits or regions separated by obvious geographical barriers (e.g. valleys) (Figure S3.3a, b).

We assigned species pairs to one of five possible discrete states, defined by the combination of sympatry/allopatry and elevation overlap/non-overlap (Figure 3.1b). For sister species occurring in allopatry, they may have overlapping (state 1) or non-overlapping (state 3) elevational ranges. Sister species occurring in sympatry may have non-overlapping elevational ranges (state 4), overlapping elevational ranges (state 5), or elevational ranges that overlap in allopatry but not sympatry (state 2). We did not classify pairs in a separate state if they showed elevational divergence in allopatry but not sympatry (opposite of state 2). Such a state would be unimportant for interactions between sister species as elevational differentiation may not be required for sympatry, or be the cause of interactions with non-sister species.

We classified sister species to each state using the following protocol: (i) We determined if pairs were allopatric or sympatric (e.g. Figure S3.3a vs S3.3i) and (ii) exhibited range-wide elevational overlap using Stotz *et al.* (1996) (and *BW* where taxonomy was outdated). (iii) Elevation ranges may vary regionally, and as a consequence species that have overlapping elevations at a range-wide scale may not overlap locally (Terborgh & Weske 1975; Graves 1988). For sympatric pairs that showed >10% range-wide elevational overlap we determined if species actually overlapped on a regional level using regional field guides covering each species' range. If (iiia) species showed <20% elevational overlap in all sympatric and allopatric regions, they were reassigned to state 4. Species were assigned to state 2 if (iiib) the sister species had overlapping elevation ranges in regions of allopatry but not sympatry (<20%) and (iiic) no other closely related species forms a hypothesised elevational replacement in the allopatric part of their range. This last step was to ensure that overlap in regions of allopatry or non-overlap in regions of sympatry was not caused by displacement from a more distantly related species. Elevational differentiation under that scenario would not be the result of interactions between the sister species. We assessed this using information on the geographic and elevational ranges of congeners in the focal region as well as observations of elevational replacing species frequently mentioned in field guides.

*Statistical analysis using Markov models*

To infer the relative importance of different assembly scenarios in explaining patterns of geographic and elevation overlap and turnover, we developed a continuous time multi-state Markov model (Figure 3.1b). In this model, the initial state for sister species is allopatry with overlapping elevational ranges (state 1), which reflects the situation expected at the time of their initial divergence (Coyne & Orr 2004). Sister pairs then stochastically transition between states, with different transition pathways corresponding to the different assembly scenarios. Under the ES model, sister species first transition to having non-overlapping elevation ranges whilst remaining in allopatry (state 3). They can subsequently transition to having non-overlapping elevation ranges and occurring in sympatry (state 4). We accounted for the possibility that species have already diverged in elevation upon speciation by including a parameter, $\gamma$, representing the probability that species arise in state 3 (Supplementary information Figure S4). Under the ED model, sister species instead transition from state 1 to having non-overlapping elevation ranges in sympatry but maintaining overlapping elevation ranges in allopatry (state 2). Finally, the EC model is described by a direct transition from state 1 to sympatry and overlapping elevational ranges (state 5).

Once sympatry between sister species is attained elevational ranges may continue to change. Sister pairs in state 2 (i.e. elevation overlap in allopatry and non-overlap in sympatry), could subsequently diverge in their elevation range in the allopatric part of their distribution (e.g. due to ecological opportunity) and thus transition to state 4. Alternatively, they could converge in their elevation range in their sympatric distribution (e.g. due to differentiation along an alternative niche axis reducing competition) and thus transition to state 5. Equally, we allow the possibility that sympatric sister species with non-overlapping elevation ranges (state 4) may subsequently converge to occur at the same elevation (state 5) (Diamond 1973). Our model thus allows for the elevation overlap (state 5) of sister pairs on the same mountain slope, which is considered to be the final state, to be attained through any of the three community assembly scenarios.

Based on the estimated time since divergence and states of sister pairs at present we used maximum likelihood (ML) (Jackson 2011) to estimate the transition rates between the states. The full model contains 7 rate parameters corresponding to the 7 possible state transitions. We also considered simpler models by, for instance, constraining the transition rate from state 1 to 2 to be equivalent to the transition rate from state 2 to 3. The simplest model has only a single rate parameter, corresponding to identical rates for all transitions. We compared model fit across all ($n$ = 877) model combinations according to AIC and report both the best model and the model-averaged parameter values of all highly supported models ($\Delta$AIC $\leq$ 2 of best model).

*Relative frequency of trajectories*

Having inferred the transition rates between states, we then used these to estimate the relative contribution of elevational displacement (ED), elevational sorting (ES), and elevational conservatism (EC) to pairs leaving state 1 and arriving in states 2, 4 and 5. Specifically, we used the inferred rates to perform 1000 posterior predictive simulations using the Gillespie algorithm for constant rates (Gillespie 1977). Under the Gillespie algorithm, transitions between states correspond to events. The simulation starts at time $t = 0$, indicating the time since divergence for all sister species. The waiting time ($\delta$) to the next event is determined by a random draw from an exponential distribution with the mean equal to the sum of all transition rates across all sister pairs, e.g. if the transition rate from state 1 to 2 (r12) is 0.05 and there are currently 5 pairs in state 1, then this transition adds 0.25 to the total rate. This rate is constant through time, but older species will have more time to experience such an event. The event that occurs at time $t + \delta$ is selected with a probability equal to the relative contribution of each rate to the total rate. This transition applies to a single species pair and this pair is chosen at random with equal weighting across all pairs that are currently in the relevant state. As we simulate forward in time, species can no longer transition if they are younger than $t$. Species pairs are introduced to the simulation at the time that they have diverged and speciated in allopatry, and the simulation continues until the present day. During the simulation we record the percentage of sister pairs passing through each of the three pathways corresponding to different community assembly models (i.e. ED, ES, and EC), and report the mean and 95% confidence intervals across simulation runs.

*Assessing model fit*

Although the model is optimised using maximum likelihood, model fit may be poor if the underlying assumptions of the model are not met. If that is the case, estimated rates will poorly reflect the empirical observations. We assessed how well the predicted transition rates can predict (*i*) the change in frequency of states through time, and (*ii*) the distribution of sister species divergence times for each state using the output of the posterior predictive simulations. To examine if the model can adequately predict state changes through time we binned species pairs in three bins of 55-56 sister pairs. We used three bins to ensure we would approximately capture any changes in the prevalence of states through time beyond increases and decreases. The prevalence of each of the five states per bin is then compared between the empirical data and 95% CI's constructed from the final prevalence of the simulated states. If the empirical prevalence falls within the 95% CI this would indicate good model fit (Figure 3.3), but large CI's likewise indicate high uncertainty. The empirical age distribution of every state was compared to the average distribution of ages across the posterior simulations.

### *Simulation tests of accuracy and precision*

Using simulations, we further evaluated the model by assessing if we can both accurately and precisely recover the transition rates. High accuracy indicates that the model is not biased towards over- or under-estimating particular transition rates. High precision indicates that the estimated rates are close to the true rates. We explored a number of different scenarios (Supplementary information Table S3.1-S3.6), designed to characterise the three different assembly models and variants of these (S1-S3), as well as a scenario assuming identical transition rates (S4) and one corresponding to the transition rates inferred from the model-averaged model fit to the empirical data (S5). For each scenario, we performed 100 replicate simulations using the observed number and ages of sister pairs. For each simulation, we then performed an identical model fitting procedure as for our empirical data, resulting in transition rate estimates according to the best and model-averaged approach per simulation. We constructed 95% confidence intervals from the estimates across the simulations for the best and model-averaged approaches. To evaluate the accuracy and precision of the rate estimation. Additionally, we determined the coverage of the model by asking how often the 95% CI of the best model for an individual simulation captured the true rates as predetermined for every scenario, and how potential error in rate estimation impacts the relative frequency of trajectories (Supplementary information Table S3.5, S3.6).

## Results

### *Empirical distribution of sister pair states*

Across the *n* = 166 sister species pairs, the majority are currently in allopatry with overlapping elevation ranges (state 1: 62%). The next most common state is sympatry with overlapping elevation ranges (state 5: 16%), with fewer pairs having non-overlapping elevational ranges and occurring in sympatry (state 4: 11%), or allopatry (state 3: 5%), or having non-overlapping elevational ranges in sympatry but overlapping elevational ranges in allopatry (state 2: 6%). The mean age of pairs that are in allopatry with overlapping elevation ranges (state 1: 2.31Myr) is younger than all other states (state 2: 3.35, state 3: 3.19, state 4: 3.88, and state 5: 3.41Myr), consistent with our assumption that is the initial state at the time of species divergence.

### *Transition rates between states*

We found that our best model contains two parameters and constrains r12, r13, r15, r25, and r45 to 0.06 (95% CI: 0.05-0.08), and r24, r34 to 0.44 (95% CI: 0.25-0.75) transitions per pair per million years. While there are 27 models that are highly supported (≤2 ΔAIC), the model-averaged rate estimates are very similar to the best model. Because of this, we focus on the model-averaged results below. The model averaged results show that the transition rate from the initial state of allopatry with overlapping elevation ranges (state 1) to non-overlapping elevation ranges, either while in allopatry (r13 = 0.06/Myr) or upon the attainment of sympatry (r12 = 0.06/Myr) is relatively slow, and similar to attaining sympatry while conserving elevational ranges (r15=0.07/Myr). Once elevational differentiation has occurred in either allopatry (state 3) or upon secondary contact (state 2), the transition to complete elevational differentiation (state 4) is relatively fast (r34=0.53/Myr and r24=0.32/Myr).

### *The relative contribution of community assembly routes*

The posterior-predictive simulations show that following speciation a similar proportion of pairs embark on the ES (32.86%, 95% CI: 21.54-44.64%), ED (29.31%, 95% CI: 17.86-41.27%) and EC routes (37.31%, 95% CI: 24.67-50.00%) (Figure 3.2b). Of the pairs with currently non-overlapping elevation ranges in sympatry (states 2 and 4), more are inferred to be generated through ED (61.99%, 95% CI: 41.93-79.31%) than ES (38.01%, 95% CI: 20.69-58.07%) (Figure 3.2c). However, confidence intervals on these estimates broadly overlap, suggesting there is little evidence that one route is more common than the other. Of the species pairs that attain overlapping elevation ranges in sympatry (state 5) almost all of these (89.29%, 95% CI: 75.84-100.0%) attain this state via the EC route rather than the ES or ED pathways (Figure 3.2d). This can be explained because although a similar proportion of pairs embark on each pathway (i.e. r12 ≈ r13 ≈ r15), species pairs taking the ES (1->3->4->5) and ED (1->2->4->5 or 1->2->5) routes must pass through a number of intermediate states to attain overlapping elevation ranges in sympatry and this takes much longer than the direct EC route (1->5). We note that relaxing our threshold at which we consider species to have overlapping elevation ranges resulted in qualitatively similar results (Figure S3.1).

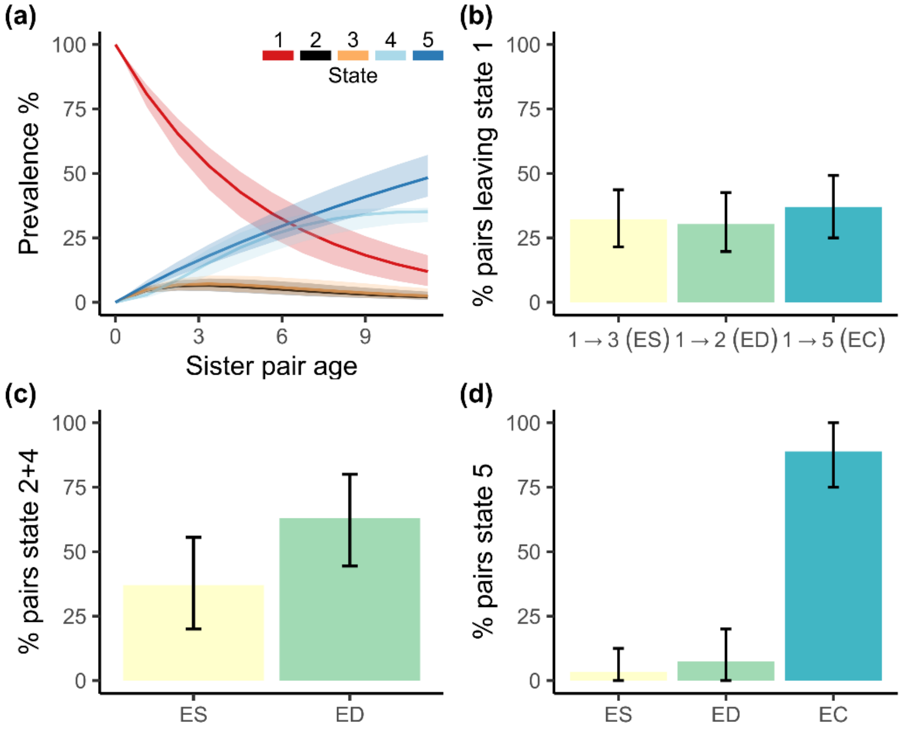

**Figure 3.2** Sister species occurrence predictions through time and trajectories taken. A) predicted prevalence of the five states, as represented in Figure 1, through time. State 2 (black) and 3 (yellow) overlap greatly in predicted prevalence. Shaded areas show 95% confidence intervals. B) Percentage of sister pairs that have left state 1 and have transitioned to state 3, 2, or 5 to either undergo elevational sorting (ES), displacement (ED), or conservatism (EC). C) the percentage of pairs gone through either ES or ED that currently occupy non-overlapping elevational ranges in sympatry. D) The percentage of pairs

that have gone through ES, ED, or EC to reach sympatric ranges with overlapping elevational distributions. Results are obtained from posterior-predictive simulations of the model-averaged parameter estimates.

*Assessing model fit and the accuracy and reliability of estimated transition rates*

Our simulations show that transition rates from state 1 (r12, r13, and r15) (Figure 1), can be reliably and accurately estimated irrespective of the simulation scenario (Table S3.1, S3.2). Later transitions (r24, r25, r34, r45) are estimated with less accuracy, probably because there are relatively few old sister pairs and thus less information to reliably estimate these rates. However, the posterior-predictive simulations under the estimated parameter values shows that this does not inherently highlight model inadequacy because we can predict the incidence of the five states well through time (Figure 3.3). The simulations capture the main patterns, namely: an increase with age of sympatric pairs that are currently not diverged in elevation (state 5), a decrease in the pairs that have not diverged in elevation and are allopatric (state 1), and slight increases for pairs that are either in allopatry or sympatry but have diverged in elevation (state 2, 3 and 4). However, our simulations also show that when we attempt to recover the trajectories taken for the empirical data, there is a bias to overvalue the contribution of ED and undervalue EC (Table S3.5, S3.6). This bias likely stems from the high uncertainty in the estimation of the transition rate between state 2 to 4 and 2 to 5. We note that this does not influence our conclusions as the percentual changes do not qualitatively change the observed patterns, and perhaps more importantly show that we do not overestimate elevational conservatism.

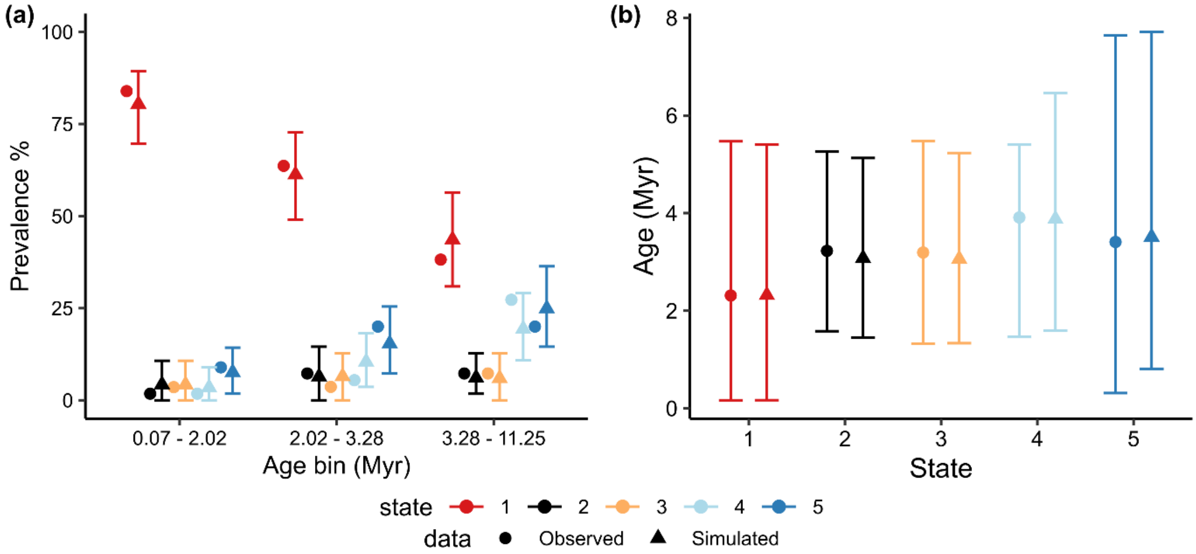

**Figure 3.3** Empirical and predicted prevalence of states through time and age distributions of states. A) Empirical (circles) and predicted (triangles) prevalence (triangles) represent the prevalence of the states within three bins of approximately equal size (n = 56, 55, and 55). Brackets represent the 95%CI of the prevalence of each state across 1000 posterior-predictive simulations. b) Empirical and predicted age distributions per state. Brackets indicate the mean and 95% CI for the empirical age distributions and the average mean and 95% CI over 1000 simulations for the predictions.

## Discussion

Multiple historical processes have been proposed to explain the patterns of range overlap and turnover across tropical elevational gradients. However, because previous studies have focused on static biogeographic patterns and treated elevational sorting, displacement and conservatism as alternative explanations, their relative contribution has remained unknown. Through our analysis of the dynamics of sympatry and elevation overlap among Neotropical montane birds, we present three key findings. First, we show that the relative contributions of different historical assembly models can be reliably inferred given current phylogenetic and geographic data among sister species. Second, our results show that elevational sorting and displacement contribute almost equally to explaining the turnover of closely related bird species across elevation gradients. Finally, we show that the overlap of sister species along elevation gradients is almost entirely (>89%) explained by species attaining sympatry while elevational ranges remain conserved, rejecting more complex scenarios requiring displacement followed by subsequent shift to occupy the same elevational range.

The high biodiversity of tropical mountains is associated with rapid turnover in community composition, as ecologically similar species replace one another up the mountain. Previous studies of montane birds have concluded that elevational displacement rather than sorting is the dominant process explaining such elevational replacements (Diamond 1973; Freeman 2015). This is because most sister pairs with divergent elevation ranges currently occur in sympatry rather than allopatry, potentially consistent with the idea that divergence happens upon secondary contact rather than during geographic isolation. However, our results suggest that the importance of elevational sorting has been underestimated. This is because species that diverged in their elevation ranges while in allopatry can subsequently transition to sympatry, thus reducing the apparent incidence of allopatric pairs with divergent elevational ranges. Our phylogenetic model accounts for these historical dynamics and shows that elevational sorting and displacement contribute approximately equally to explaining turnover among sister species across tropical elevation gradients.

While our analysis detects evidence of both elevational sorting and displacement, we find that sympatry is frequently reached without differentiation in elevation. We estimate ~44% of sister species living on the same mountain slope attain sympatry while conserving their ancestral elevation range. Such a high frequency of conservatism may not seem surprising, given that previous studies focussed on the drivers of speciation have shown that most vertebrate sister species have overlapping elevation ranges (Cadena *et al.* 2011). However, a high frequency of elevation overlap among sister species is by itself inconclusive regarding the mode of community assembly because the same pattern can arise under the elevational displacement model if the initial constraints on elevational overlap weaken as species diverge across alternative niche axis (e.g. resource use). Our phylogenetic approach to modelling the dynamics of elevation range overlap, enables us to exclude this possibility. Indeed, we estimate that displacement and subsequent overlap in species elevational ranges contributes little (6.45%) to current patterns of co-occurrence along elevation slopes.

Our finding that a high proportion of allopatric sister species directly transition to occupy overlapping elevations in sympatry need not suggest that competition or other negative species interactions are unimportant in limiting coexistence for these species. Indeed, evidence that interspecific competition limits elevational ranges is widespread in birds (Terborgh & Weske 1975; Freeman & Montgomery 2016; Freeman *et al.* 2016, 2019). Instead, species attaining sympatry without diverging in their elevation range may have diverged across alternative niche dimensions such as resource or microhabitat use. Such an explanation would be consistent with previous evidence that coexistence of Neotropical bird species following speciation is limited by rates of divergence in key trophic traits, such as beak size (Pigot *et al.* 2018). Furthermore, the relative mix of different assembly processes may not be static over geological time. Given the relatively young age of many Neotropical montane radiations, and that there is little evidence for a slowdown in the rates of diversification (Weir 2006; Harvey *et al.* 2020), local niche space at any point along the elevational gradient may currently be far from saturated. As niches become increasingly densely packed over time, it is possible that elevational sorting and displacement may become increasingly important routes to sympatry as has been suggested for New Guinean (Diamond 1973) and Himalayan songbirds (Price *et al.* 2014).

The relative mix of elevational sorting, displacement and conservatism inferred by our models pertains to Neotropical birds and the dynamics of community assembly may differ in other tropical mountain systems that have different geographic configurations and histories of uplift. However, we note that we obtained very similar results when re-analysing a global dataset of avian sister species (albeit skewed towards the Neotropics) (Fig. S3.2), suggesting that our conclusions may apply across tropical mountain regions generally. Another possible critique of our approach, is that by focussing on elevational ranges we have neglected to consider that elevation itself might be plastic but that other processes such as habitat availability, temperature, and humidity might be what creates the elevational range for most species. However, we consider it unlikely that this could completely explain our results as elevational ranges remain highly conserved between and within species. We do concur that this is an important avenue of future research of which our approach is a first conservative attempt.

A sister pair approach is advantageous because we can make simplifying assumptions about the initial state, but we also miss evolutionary dynamics occurring above this taxonomic level. For instance, in our analysis we see sympatry with overlapping elevations, as an absorbing state but not all pairs end up in this state. Beyond differential completion times for each process, speciation may interfere, because speciation effectively results in a new pair of sister species that may transition to sympatry. Indeed, species that form elevational replacements along mountain slopes are often not sisters (Patton & Smith 1992; García-Moreno & Fjeldså 1999; Caro *et al.* 2013). Estimating the frequency of sorting and displacement might thus require information about what happens after speciation.

To understand if speciation introduces any bias in the estimation of relative frequencies we need to consider (*i*) when speciation is more likely to occur, and (*ii*) when sorting and displacement are more likely to occur. First, on the one hand, speciation might disproportionally break up the processes of sorting and displacement compared to conservatism because they take more time. On the other hand, speciation may depend on range expansion, increasing the likelihood for speciation under conservatism as sympatry has been attained (Weir & Price 2011). This might mean that we observe less sister species with conserved elevational ranges instead. Second, sorting and displacement could still be completed between non-sister species. This could mean that we underestimate the contribution of sorting and displacement to sympatric diversity within individual elevational zones. However, this is also unlikely to fully explain our results because it is among young, ecologically similar species that competition and other negative species interactions are expected to be strongest. We thus conclude that the sister pair approach might not clearly bias our results in any direction and that future research will need to focus on dissecting how these processes operate beyond sisters.

The expansion of species ranges following speciation is an essential step not only in the build-up of sympatry but also in providing renewed opportunities for further rounds of geographic isolation and thus the generation of new species (Weir & Price 2011). Our results show that the rate of range expansions leading to sympatry are substantially accelerated by the capacity for species to occur on the same slope without having to first diverge in their elevation range. Specifically, according to our models, the expected lag time to sympatry among sister species that have retained overlapping elevational ranges (14.21Myr), is substantially shorter than the lag time for species passing through the elevational sorting or displacement routes combined (18.06Myr). Thus, in addition to the turnover of species across elevations, a key additional ingredient explaining the high diversity of tropical mountains is the capacity for species to coexist locally without having to diverge into different elevational zones.

Our model represents a simplification of the complex processes governing the assembly of montane biotas and is limited to explaining the patterns of sympatry and elevation overlap among sister species. However, to our knowledge this is the first study to quantify the relative frequency of elevational sorting, elevational displacement, and elevational conservatism in shaping species distributions across montane gradients. A key next step will be to test how well our results generalise to different mountain regions or taxa that vary in their ecology. Such a comparative approach may be necessary to uncover why elevational sorting and displacement appear to be relatively rare between the species where we expect them to be most common. Our model could also be applied To disentangle the dynamics of assembly across other ecological gradients and evolutionary radiations, such as the vertical layering of foraging niches among rainforest birds (MacArthur 1958), perch height among Anolis lizards (Lister 1976), or depth zonation in the Cichlid fish of East African rift lakes (Rodríguez & Lewis 1997).

## Chapter 4:

# Priority effects and the macroevolutionary dynamics of biodiversity

### Abstract

Priority effects can play a fundamental role in the assembly of ecological communities, but how they shape the dynamics of biodiversity over macroevolutionary timescales remains unclear. Here we develop a metacommunity model combining local priority effects with niche evolution, speciation and extinction. We show that by promoting the persistence of rare species, local priority effects cause the evolution of higher metacommunity diversity as well as major disparities in richness among evolutionary lineages. However, we also show that classic macroevolutionary patterns of niche incumbency—whereby rates of regional diversification and invasion slow down as ecological niches are filled—do not depend on local priority effects, arising even when invading species continuously displace residents. Together, these results clarify the connection between local priority effects and the filling of ecological niche space, and reveal how the impact of species arrival order on competition, fundamentally shapes the maintenance and generation of biodiversity.

### Introduction

Ecological communities are often assembled from the sequential invasion of species with the order of species arrival playing a potentially critical role in determining the outcome of ecological interactions (Fukami 2015; De Meester *et al.* 2016). The impacts of arrival order are generally discussed in terms of inhibitory priority effects (hereafter 'priority effects') (MacArthur 1972), whereby resident species—by filling ecological niche space (Westoby *et al.* 1989; Odion *et al.* 2010)—preclude the invasion of later arrivals. Priority effects have been documented in many systems and can fundamentally alter the composition, diversity, evolution and functioning of ecological communities (Chase 2003; Urban & De Meester 2009; Fukami 2015; White *et al.* 2021). Extended over macroevolutionary timescales, priority effects—often referred to as 'niche incumbency'—have been invoked to explain many of the major features of biodiversity (Valentine *et al.* 2008), from the succession of evolutionary dynasties following mass extinction events (Hull 2015), to the unfolding of adaptive radiations (Stroud & Losos 2016; Gillespie *et al.* 2020). Yet, how priority effects shape patterns of species diversification remain poorly understood because theory bridging this ecological and macroevolutionary divide is lacking.

According to the idea of niche incumbency, an early radiating or dispersing lineage fills available ecological niche space, inhibiting the diversification of other lineages until extinction of the incumbent leads to renewed ecological opportunity (Rosenzweig & McCord 1991; Alroy 1996). This model provides a potentially compelling explanation for disparities in species diversity between early and later originating clades (Hull 2015), and why rates of diversification in adaptive radiations slow down over time (Weir 2006; Price 2008; Rabosky 2013). Specifically, as species richness accumulates, local ecological niche space becomes filled, inhibiting the expansion of newly formed lineages, leading to a decline in average species range size or abundance and thus higher rates of extinction and reduced opportunities for further speciation (Weir & Price 2011; Pigot *et al.* 2018).

Yet, the extent to which these signatures of niche incumbency at the macroevolutionary scale arise from local priority effects *per se* is unclear. One possibility is that rather than occupied ecological niches resisting invasion, invading species may displace ecologically similar residents. This scenario forms a cornerstone of the 'taxon cycle' model, in which metacommunity species richness may be constant over time, but invasions drive a continual waxing and waning of species distributions and turnover in local composition (Wilson 1959; Ricklefs & Bermingham 1999; Economo & Sarnat 2012; Pepke *et al.* 2019). According to this model, the ‘pressure of competition’ on species abundance and distribution may still inhibit species diversification, but this occurs without local residents having any ‘home-field advantage’.

Here, we examine how local priority effects shape the dynamics of biodiversity over macroevolutionary timescales by performing a computational experiment of an evolving metacommunity. In this model, species arise through speciation, evolve in their ecological niche within a bounded niche space and disperse to colonise new sites. Competitive exclusion caused by niche similarity occurs within sites, with the order of species arrival determining the outcome of competition. Specifically, we simulate a model of resident-superiority (RS), characterising a local priority effect, in which species longer established at a site drive the local extinction of more recent invaders. We compare this to a model of invader-superiority (IS), in which more recent invaders drive the local extinction of longer established residents, akin to the taxon cycle model. Finally, we examine an intermediate scenario of symmetric competition (SC), in which the probability of local extinction depends only on niche overlap and is independent of local arrival order.

We note that these different competition scenarios could arise through a variety of demographic and ecological routes. For instance, local priority effects may arise because residents have a numerical advantage (Hubbell 2001), modify niche space (Westoby *et al.* 1989; Odion *et al.* 2010), or because invaders are subject to Allee effects (Henriques-Silva *et al.* 2019). On the other hand, invaders may have a transient competitive advantage if they have escaped from their natural enemies (enemy release hypothesis (Keane & Crawley 2002; Colautti *et al.* 2004)) or carry novel weapons (e.g.

pathogens (Diez *et al.* 2010; Lymbery *et al.* 2014; Vilcinskas 2015; Sheppard & Schurr 2019)). Rather than modelling these underlying processes, we instead model the effect of arrival order on the outcome of competition directly, thus enabling us to identify the unique role of local priority effects on macroevolutionary dynamics while holding all other factors constant. In particular, we focus on establishing how local priority effects shape the temporal dynamics of species diversification, metacommunity species richness and how richness is partitioned across clades. Through this, we aim to disentangle the macroevolutionary consequences of local priority effects *per se*, versus the more general effects of competition on the evolution of biodiversity.

## Methods

### *Modelling community assembly and diversification dynamics*

To investigate the macroevolutionary impact of local priority effects we develop a stochastic discrete-space, continuous-time simulation model of colonisation ($\gamma$), speciation ($\lambda$), population extinction I and niche evolution ($\sigma$). The simulation starts with a single lineage occupying a randomly selected site within a square lattice (5 x 5 sites), where each site may be thought of as a separate habitat patch, island or region that is sufficiently small that *in-situ* cladogenetic speciation does not occur (Kisel & Barraclough 2010). We also explore the effects of a larger lattice and assuming the lineage initially occupies all sites (Fig. S4.1, Appendix 4.I). We refer to each occupied site in a species' geographic range as a population. Colonisation occurs at per-population rate $\gamma$, and is modelled by randomly selecting a population from any species to disperse and then randomly selecting, for colonisation, an adjacent site (i.e. sharing an edge) unoccupied by that species. For computational efficiency only populations with adjacent sites unoccupied by the focal species can disperse, thus avoiding simulating the re-invasion of already occupied sites. To examine the effects of dispersal limitation, we also explore a scenario where any unoccupied site can be invaded rather than only adjacent sites (Fig. S4.1, Appendix 4.I).

Speciation occurs at per-population rate $\lambda$ and is modelled by randomly selecting a single population from any species to become a new lineage. For species consisting of multiple populations, speciation leads to an increase in metacommunity species richness (i.e. cladogenesis). If a species consists of a single population, it undergoes anagenetic speciation, whereby the species identity changes but there is no increase in species number. The ‘budding-off’ of a single population is perhaps most consistent with a peripatric speciation-mode (Coyne & Orr 2004) and can lead to an initially high asymmetry in range size between sister lineages (Pigot *et al.* 2010). To investigate how the initial range size asymmetry influences dynamics, we also consider a ‘vicariance scenario’, simulated by splitting the species’ range into two approximately equal size areas (Fig. 4.4, Appendix 4.I).

Species’ niches, representing the ecological requirements of a species (e.g. seed sizes consumed by a granivorous bird) (Elton 1927), are modelled as Gaussian distributions with optimum, $x_i$, and constant niche breadth $s$. All populations within a species have an identical niche optimum and breadth. Species niche optima (ancestral species $x_i = 0$) evolve over time according to Brownian motion with rate parameter $\sigma$. Niche space experiences soft evolutionary bounds at distance $K$ and $-K$ ($K = 5$) from the centre of niche space, meaning that species may evolve beyond distance $K$ or $-K$ but will experience repulsion ($\alpha = 1$) back towards the boundary (Nicolau 2002; McInnes *et al.* 2011; Thomas *Pers. Comm.*). This model can be biologically interpreted as an adaptive zone within which species are free to evolve but where fitness rapidly drops off beyond the boundary (Simpson 1953). Under this bounded model of niche evolution, metacommunity richness is expected to reach a dynamic equilibrium because of the finite number of sites and constraints on the niche similarity of coexisting species. To examine the effects of assuming strict ecological limits we also explore an unbounded niche space scenario (Fig S4.1, Fig S4.6, Appendix 4.I).

*Modelling the effects of niche overlap and arrival order on population extinction*

Populations suffer extinction at per-population rate *E* with the extinction of a species occurring when its last population is extirpated. *E* is a summation of the rate of population background extinction events $\mu_{bg}$ which is constant across populations and over time, and also the rate of population competitive exclusion $\Omega$,

$$E_i = \mu_{bg} + \Omega_i$$

where $\Omega$ depends on a constant $\mu_{comp}$ and the niche overlap (*OVL*) between the focal species (*i*) and other residents at a site:

$$\Omega_i = \mu_{comp}\left(\frac{OVL_i^{\beta}}{OVL_i^{\beta} + \psi^{\beta}}\right)$$

Shape parameter $\beta$ was set *a priori* ($\beta = 30$) so that $\Omega$ follows a sigmoidal increase with increasing *OVL*. This corresponds to a model of limiting similarity where the duration of coexistence declines rapidly beyond a threshold of niche overlap $\psi$ (Pigot and Etienne 2015). The overlap between Gaussian distributions is given by the cumulative normal function Φ and is equal to $2\Phi\,(-\,|x_i\,-\,x_j|/2s)$, where $x_i$ and $x_j$ are the respective niche optima and *s* the niche breadth (Inman & Bradley 1989; Clarke *et al.* 2017). *OVL* is modelled as the unique intersection of the cumulative normal distributions of species *i* and, $j_1$ and $j_2$, the two resident species that are its immediate neighbours in niche space (i.e. the species with the nearest positive and negative niche optima):

$$OVL_i = \sum_{n \in \{nearest\ neighbours\}} 2\Phi\left(-\frac{|x_i - x_{j_n}|}{2s}\right) - 2\Phi\left(-\frac{|x_{j_1} - x_{j_2}|}{2s}\right)$$

Here the first term refers to the summed overlap between focal species *i* and its nearest neighbours and the second term to the overlap between the nearest neighbours. We only consider nearest neighbours (Fig. 1) as the niches of all species have identical width, and therefore *OVL* denotes the total overlap in niche space, which leaves–1 - *OVL* as the unique niche space occupied by the focal species. Biologically, we interpret this unique niche space as the uniquely exploited resources by which a population can sustain itself. However, our model could be extended to consider diffuse competition (Nuismer & Harmon 2015).

To address the effect of arrival order on competition we track the timing of species colonisation at each site (Fig. 4.1). Following both anagenetic and cladogenetic speciation, newly formed species retain the arrival times of the parent species at the sites where they occur. When a species recolonises a site where it had previously become extinct, the time since arrival for this species is reset to zero. Under resident-superiority (RS), we disregard the niche overlap *OVL* from species that arrive later than focal species *i*, thus reducing the strength of competition experienced by longer standing residents (Fig. 4.1a). In contrast, under invader-superiority (IS), we disregard the niche overlap *OVL* from species that arrived earlier than focal species *i*, thus reducing the strength of competition experienced by recent invaders (Fig. 4.1b). In the symmetric competition model (SC) the focal species experiences competition from either the earlier or later arriving species selected at random. In this way we keep the identity of competitors and intensity of competition the same, but disregard arrival order when determining the outcome of competition (Fig. 4.1c; Appendix 4.II).

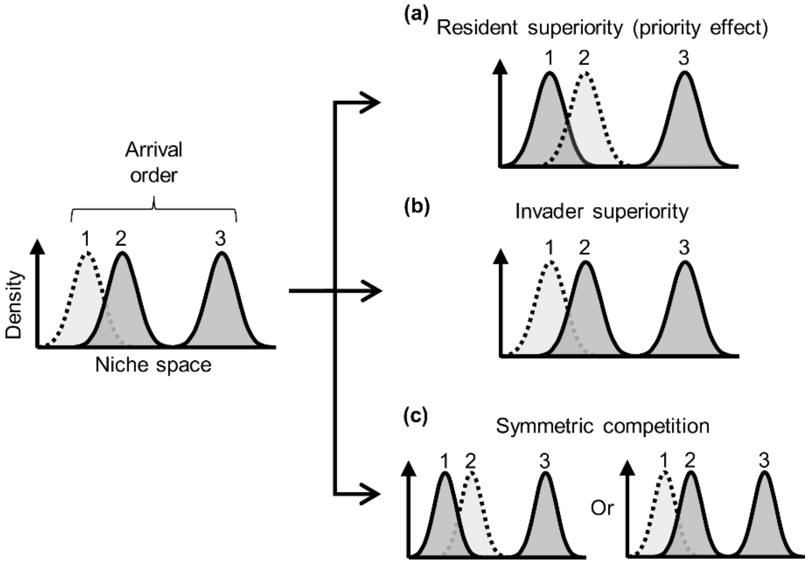

**Figure 4.1** The impact of arrival order on the outcome of competition. An exemplary community is represented consisting of three species with niches distributed across an arbitrary axis and competition occurring between nearest neighbours. The order of arrival presented here is arbitrary (i.e. unrelated to niche position), and is denoted above each species, with 1 indicating the first species to arrive and 3 the last species to arrive. The identity of the species that is excluded from the community by competition (dashed species) depends on both niche overlap and the order of arrival according to three alternative scenarios: a) resident-superiority, where the species that arrived earlier outcompetes the neighbouring species that arrived later driving it locally extinct; b) invader-superiority, where the species that arrived later outcompetes the neighbouring species that arrived earlier; and c) symmetric competition, where competitive exclusion is independent of arrival order and only dependent on overlap in niche space.

### *Exploration of parameter space and summary statistics*

We simulated the model in continuous time using the modified Gillespie algorithm (Gillespie 1977; Allen & Dytham 2009)(Appendix II). For each of the three models of competition, we examine varying rates of (*i*) speciation ($\lambda$ = 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64), (ii) population background extinction ($\mu_{bg}$ = 0, 0.005, 0.0125, 0.025, 0.05, 0.075, 0.125), (*iii*) rate of niche evolution ($\sigma$ = 0.125, 0.25, 0.50, 0.75, 1.00, Fig. S2), and (*iv*) the level of niche overlap at which the rate of local competitive exclusion $\Omega$ is half $\mu_{comp}$ ($\psi$ = 0.125, 0.25, 0.5, 0.75, 0.875, Fig. S3). We keep species niche breadth ($s$ = 0.15), colonisation rate ($\gamma$ = 0.25) and the constant controlling the rate of competition exclusion ($\mu_{comp}$ = 5) fixed, as their effects are expected to be partially redundant with other parameters. For instance, increasing the colonisation rate $\gamma$ will have a similar effect to reducing the rates of speciation $\lambda$, population background extinction $\mu_{bg}$ and niche evolution $\sigma$, while increasing niche breadth $s$ would have a similar effect to reducing $\psi$ or increasing $\mu_{comp}$.

Throughout we record composition at each site, metacommunity and site-level species richness, species range sizes (i.e. number of occupied sites) and phylogenetic relationships. We track the actual rate of colonisation and population extinction over time and use the complete fossil phylogeny to calculate the rate of species extinction and cladogenetic speciation (hereafter, ‘speciation’) (Ezard & Purvis 2009). Subsequently, diversification rate is calculated as the speciation rate minus extinction rate in the fossil phylogeny and the rate of branching in the reconstructed phylogeny (i.e. containing only extant species). Rates are reported as either the ‘metacommunity rate’ (i.e. the total across the metacommunity), the average ‘per-lineage rate’, or, when accompanied by the corresponding model parameter symbol, the ‘per-population rate’ used as model input. From the reconstructed phylogeny, we calculate phylogenetic imbalance using the Sackin index. Positive (negative) values indicate a more uneven (even) distribution of species among lineages than expected under a constant rate pure-birth model of speciation (Appendix III)(Blum & François 2005). Simulations are terminated when either (*i*) all species have gone extinct, or (*ii*) the elapsed time $T$ is reached. Based on preliminary simulations we set $T$ = 360 to ensure we reach a stochastic equilibrium in each parameter and metric. To establish identical (fossil) crown ages we track time starting at the first cladogenetic speciation event. To allow diversification patterns to be meaningfully summarised, simulations resulting in fewer than three extant species at time *T* were repeated, although under the chosen parameters this rarely occurred. Simulations are repeated until we obtain 100 successful realisations for each parameter combination. These realisations are used to investigate the null hypothesis that diversification dynamics are independent of the presence of priority effects.

## Results

### *Temporal dynamics of species richness*

Under all competition scenarios (resident-superiority, invader-superiority and symmetric competition), species richness follows a similar temporal trajectory at both the metacommunity and local level (Figs. 4.2, S4.1-S4.3). Early in the radiation, richness accumulates rapidly (Fig 4.2j) because most sites contain few if any species, rates of population extinction are lower than rates of colonisation (Fig. 4.2a-b), and species average range size thus expands (Fig. 4.2i). This leads to low rates of species extinction and an accelerating rate of speciation at both the metacommunity and lineage level (Fig. 4.2c, g). As local richness accumulates, there is an increase in the rate of population extinction (Fig. 4.2e), eventually converging on the rate of colonisation (Fig. 4.2f), so that average range size peaks and subsequently declines (Fig. 4.2i). The decline in average range size causes an increase in per-lineage rate of species extinction, decrease in speciation (Fig 4.2g), and a decline in the metacommunity and per-lineage rate of diversification (Fig 4.2d, h). While a diversification slowdown is also evident in the reconstructed phylogeny, this pattern is eroded over time under IS and SC as high rates of species extinction prune the oldest lineages from the tree (Fig. S4.4d). Eventually local sites, and then the metacommunity, reach a dynamic equilibrium in which species richness fluctuates stochastically around a steady state (Fig 4.2j).

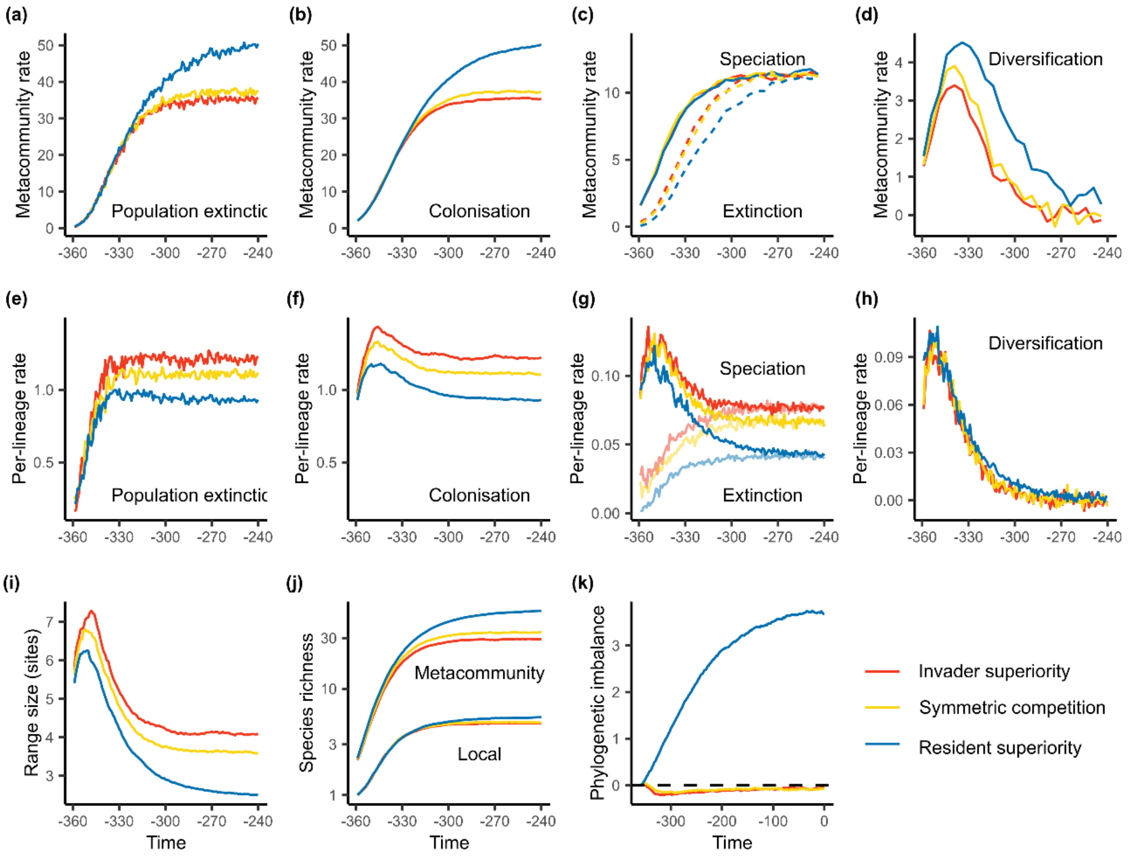

**Figure 4.2** The dependence of macroevolutionary dynamics on the presence or absence of priority effects. Priority effects are represented by the RS model (blue) and is compared to the opposite scenario of IS (red) and an intermediate SC (yellow) model, where the probability of competitive exclusion is independent of arrival order. Each plot shows the results for a different macroevolutionary rate or pattern, with the x-axis representing the time from the crown age to the present day. a-d) total metacommunity rate and e-h) mean per-lineage rate of a,e) population extinction; b,f) colonisation; c,g) cladogenetic speciation (bold) and species extinction (dashed/shaded); d,h) diversification; i) average range size; j) metacommunity and average local species richness; k) Sackin index of phylogenetic tree imbalance, where the dashed line represents the imbalance expected under a pure-birth model. Values show the mean trend for 500 replicate simulations under: $\psi$ = 0.25, $\lambda$ = 0.02, $\gamma$ = 0.25, $\sigma$ = 0.25, and $\mu_{bg}$ = 0. Parameter values are representative of the general dynamics and result in the highest relative difference in species diversity between IS and RS. See Appendix III for details on metrics used.

### *Metacommunity and local species richness*

Although the temporal accumulation of species richness is qualitatively similar across competition scenarios, local and metacommunity richness varies (Fig. 4.2j). Equilibrium species richness, at both local and metacommunity scales, is highest under the RS model, lowest under the IS model, and intermediate for the SC model (Figs S4.1-S4.3). These differences in richness arise despite each model being governed by identical ecological limits and parameters, and is due to the substantially faster rate of species extinction in the SC and IS models (Figs. 4.2c, g, 4.3). When invaders can displace residents, species occupying a single site can be driven to extinction. In contrast, when priority effects operate these rare species are resistant to competitive displacement and so, notwithstanding stochastic background extinction, can accumulate in the metacommunity (Fig. 4.3). The persistence of these rare species boosts the total number of populations in the metacommunity leading to higher metacommunity rates of population extinction and colonisation under the RS model (Fig. 4.2a-b), but lower per-lineage rates of population extinction, colonisation and speciation (Fig. 4.2e-g). Because single-site endemics only undergo anagenesis, metacommunity rates of speciation are unaltered by the persistence of rare species and are thus similar across models (Fig. 4.2c).

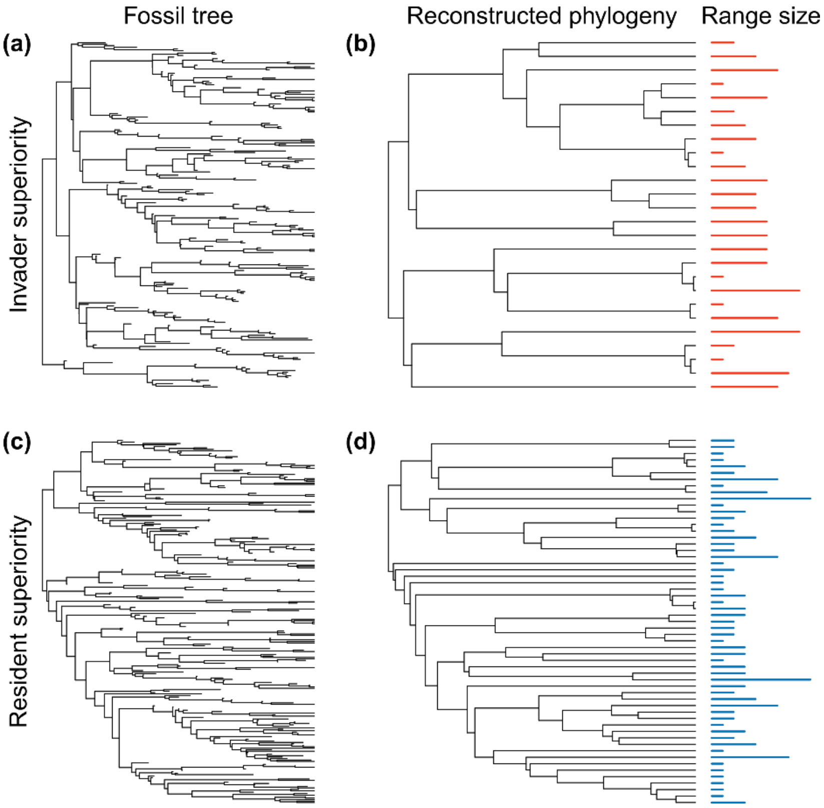

**Figure 4.3** The impacts of priority effects on diversification dynamics. Phylogenetic trees from a single exemplar simulation are shown for respectively the IS (a-b) and RS (c-d) model. In (a, c) fossil trees are shown including extinct lineages, while (b,d) show the reconstructed phylogeny (i.e. including only extant lineages). Coloured bars at the tips of the phylogeny in (b,d) indicate the species range sizes at the present. The exemplar trees were simulated under the following parameter values: $\psi$ = 0.25, $\lambda$ = 0.02, $\gamma$ = 0.25, $\sigma$ = 0.25, and $\mu_{bg}$ = 0.

The higher metacommunity richness under the RS model is evident across a broad region of parameter space (Figs. S4.1-S4.3), but varies according to key model parameters (Fig. 4.4). With high rates of population background extinction $\mu_{bg}$, the strength of priority effects is reduced leading to more similar metacommunity richness across competition scenarios (Fig. 4.4). In contrast, when the rate of speciation $\lambda$ is low relative to the rate of colonisation $\gamma$ the relative metacommunity richness of the RS model is increased. This is because species with similar ecological niches rapidly come into contact following speciation leading to faster species extinction in the SC and IS models. The role of priority effects in boosting richness by reducing species extinction is highlighted by comparing a peripatric and vicariance speciation-mode (Fig. 4.4). With vicariant speciation, fewer single-site endemics that are vulnerable to extinction are generated, and thus although still present, the difference in metacommunity richness between the RS and IS (and SC) models is reduced (Figs. 4.4, S4.1).

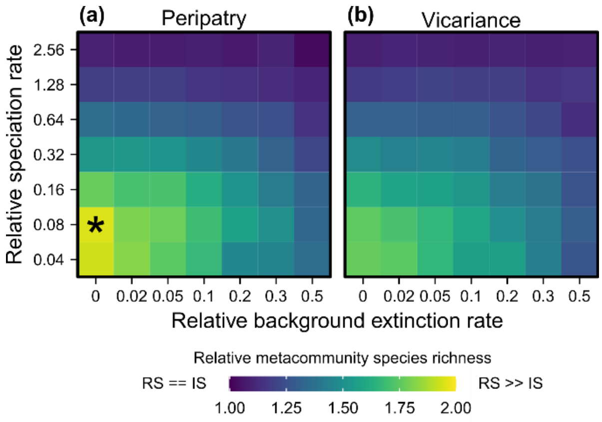

**Figure 4.4** The influence of the rate of population background extinction, speciation and speciation-mode on the relative species richness expected under the IS and RS model. a) peripatric speciation-mode and b) vicariance speciation-mode. On each plot, the y-axis and x-axis denote the speciation $\lambda$ and population background extinction $\mu_{bg}$ rates respectively, both calculated relative to the rate of colonisation, kept constant at $\gamma = 0.25$. Colours indicate the ratio between the average metacommunity richness for the RS and IS model calculated across 100 replicate simulations at $T = 360$. The parameters used in figure 2 are highlighted with an asterix (*). Competitive intensity ($\psi = 0.25$) and rate of trait evolution ($\sigma = 0.25$) are kept constant for all simulations.

## Phylogenetic tree imbalance

Priority effects have a major impact on phylogenetic imbalance (Fig. 4.3). In the IS and SC models, phylogenies are more balanced than expected under a pure-birth model (Fig. 4.2k). This is because species on phylogenetic branches that have diversified more rapidly will experience more intense competition from relatives, leading to smaller species ranges and thus lower rates of speciation and higher rates of species extinction. This negative feedback on diversification leads to a more even distribution of richness among clades (Fig. 4.2k). In contrast, under the RS model, phylogenies may either be more unbalanced or balanced than a pure-birth model depending on the speciation-mode (Fig. 4.5b, d).

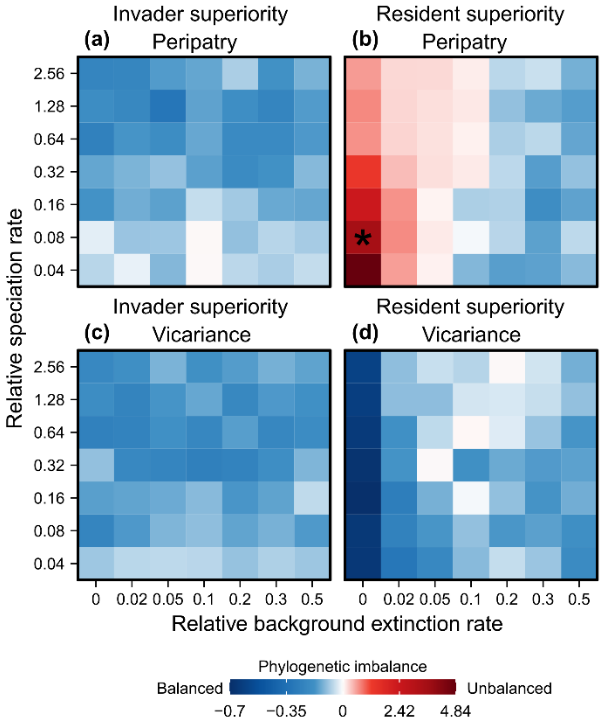

**Figure 4.5** The influence of the rate of population background extinction, speciation and speciation-mode on phylogenetic tree imbalance expected under the a,c) IS b,d) and RS model and under a-b) peripatric and c-d) vicariant speciation modes. On each plot, the y-axis and x-axis denote the rate speciation $\lambda$ and population background extinction $\mu_{bg}$ respectively, both calculated relative to the rate of colonisation, kept constant at $\gamma$ = 0.25. Colours indicate the Sackin index of phylogenetic tree imbalance. To better visualise patterns, negative (blue = balanced) and positive (red = unbalanced) values of the Sackin index were rescaled by the highest balance or imbalance values respectively before plotting. The parameters used in figure 4.2 are highlighted with an asterix (*). Competitive intensity ($\psi$ = 0.25) and rate of trait evolution ($\sigma$ = 0.25) are kept constant for all simulations.

With peripatric speciation, species with large geographic ranges undergo faster rates of speciation, producing multiple daughter species which initially occupy only a single site. Under the RS model, these rare species are unable to expand their range until they have diverged sufficiently in their niche to coexist with the parental lineage, but are also relatively resistant to extinction. Thus, by enforcing differences in range size generated during speciation, priority effects lead to large asymmetries in rates of diversification across lineages and thus unbalanced trees (Figs. 4.2k, 4.3, 4.5b). In contrast, with vicariant speciation, sister lineages have similar range sizes and thus rates of diversification. This symmetry is enforced by priority effects leading to balanced trees (Fig. 4.5d). The impact of priority effects on phylogenetic tree shape vary depending on rates of population background extinction $\mu_{bg}$ and speciation $\lambda$. When population background extinction is rapid $\mu_{bg}$ the impacts of priority effects are eroded, leading to trees that converge on similar levels of balance to the IS and SC models (Fig. 4.5a, b). Equally, when speciation $\lambda$ is rapid relative to colonisation $\gamma$, the impacts of priority effects in driving extreme tree shapes is reduced. This is because species are unable to spread and attain large ranges before speciating, reducing among lineage heterogeneity in range size and thus equalising rates of diversification. This latter scenario may characterise oceanic islands when colonisation events are rare, but speciation then proceeds rapidly due to an absence of gene flow.

## Discussion

Local priority effects have been identified as an important process in understanding the assembly and diversity of ecological communities (Fukami 2015). However, the impact of local priority effects on the origins and maintenance of biodiversity over macroevolutionary timescales has remained unclear. Here we bridge this gap, by developing a theoretical model of an evolving metacommunity in which the presence of local priority effects can be modified in order to identify their unique role in generating broad-scale macroevolutionary patterns. We demonstrate that while the temporal dynamics of species accumulation is remarkably insensitive to the existence of local priority effects, they can profoundly shape metacommunity species richness and how this richness is partitioned among clades.

Our model assumes that metacommunity richness is subject to ecological limits, set by the finite number of local sites and limits to niche similarity among coexisting species. When clades evolve under these conditions, our model produces the classic signature of an adaptive radiation, whereby rates of diversification slow down over time and clades approach an equilibrium species richness (Rabosky 2009; Moen & Morlon 2014). This pattern is often attributed to 'niche incumbency', in which early evolving species pre-empt ecological niche space (Price *et al.* 2014). This verbal model of niche incumbency is best captured by our resident-superiority scenario, in which longer established resident species benefit from a local priority effect and deterministically exclude more recent invaders with similar ecological niches. However, our results show that a slowdown in diversification rate does not require—and thus does not provide evidence for—the existence of local priority effects because the same temporal pattern arises even when more recent invaders stochastically (symmetric competition), or deterministically (invader-superiority), displace residents.

Under the resident-superiority model, as niche space becomes more densely packed, the invasion of local communities is increasingly inhibited, resulting in average species range size declining as new species arise but are unable to expand. In contrast, when invading species are competitively equivalent (symmetric competition) or superior (invader-superiority) to residents, there is a constant turnover in the identity of species occupying a site, as new lineages arise, invade and displace residents. Species originating later in the radiation can just as readily invade a site as could species at the start of the radiation. Yet, despite these contrasting dynamics, the effects of heightened competition in depressing the average range size of species is the same. When invading species are competitively equivalent or superior, then as niche space becomes increasingly densely packed, the gain in range size made by one species invading a site is balanced by a reduction in the range size of the resident species that the invader displaces. In addition, the benefits of being an invader are temporary, because recent invaders to a site will themselves become longer established residents and in turn be displaced (Sheppard & Schurr 2019). Thus, over time, increasing niche packing drives a similar decline in average range size, and a concomitant reduction in speciation rate and increase in species extinction rate, regardless of whether local priority effects operate or not. This conclusion is not dependent on assuming a strict ecological limit to metacommunity diversity, because we find the same result when ecological niche space is unbounded (Fig. S4.1, S4.6).

In addition to a temporal slowdown in diversification, the resistance of more diverse systems to external invasion has also been taken as evidence for local priority effects (Gillespie 2004; Brockhurst *et al.* 2007; Fukami *et al.* 2007; Betancur-R. *et al.* 2012; Tanentzap *et al.* 2015). To test this possibility, we conducted a *post hoc* analysis in which we tracked the survival of an introduced alien lineage—and its descendants—originating from outside the metacommunity (Appendix 4.IV). We found that across all competition scenarios, the survival time of the invading alien lineage is lower when introduced later in the radiation (Fig. 4.6). Under resident-superiority, this is unsurprising because when niche space is densely packed, the alien lineage will be quickly outcompeted by an ecologically similar resident. By contrast, while the alien invader will always displace the local competitor under invader-superiority, its chance of long-term survival is also diminished because it can in turn be displaced, and thus potentially driven extinct, by another invader originating from within the metacommunity. Such a reduction in survival time, would be seen as a reduction in invasion success (Duncan *et al.* 2019) and implies that when local priority effects are absent, a form of priority effect (e.g. numerical dominance) can emerge at the scale of the entire metacommunity.

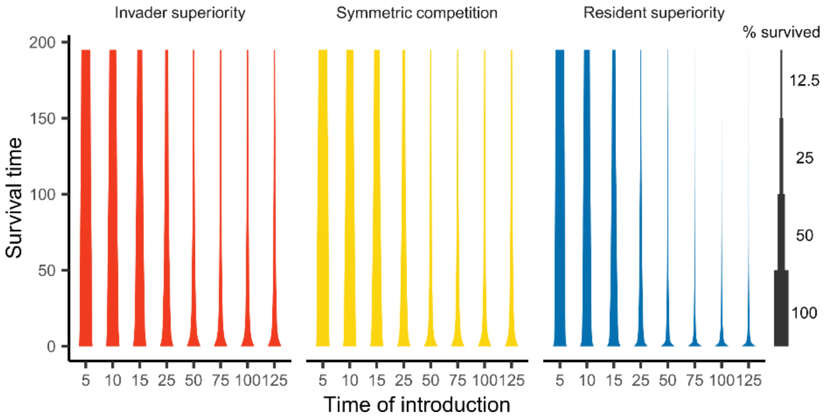

**Figure 4.6** The success of invaders from outside the metacommunity in the presence and absence of priority effects. Colours represent the three modes of competition: IS (red), SC (yellow), and RS (blue). The x-axis indicates the time from the start of the simulation when an invader from outside the metacommunity is introduced. The y-axis indicates the survival time of the invader or any of its descendent lineages. Bar width indicates the percentage of *n* = 1000 invaders that are extant at that time. A rapid decrease in bar width indicates a reduced survival time of invaders and thus lower invasion success. See Appendix 4.IV for further details.

While neither the temporal accumulation of species during adaptive radiations nor the greater resistance of diverse regions to invasion provide evidence of local priority effects, we find that other commonly observed macroevolutionary patterns do depend on how arrival order within sites alters competitive outcomes. The tree of life is highly unbalanced, with most species concentrated in a few highly diverse clades, indicating substantial heterogeneity in net diversification across lineages (Mooers &

Heard 1997; Blum & François 2006). Our results show that when ecological niches are limited but invaders can displace residents, phylogenies are more balanced than expected under a pure-birth model. This is because lineages which diversify more rapidly experience more intense competition, leading to a negative feedback on further diversification. However, when priority effects are present, the opposite pattern of strong phylogenetic imbalance can arise, suggesting that priority effects may be an important factor contributing to the disparity in species richness observed across clades.

Our results further show that this imbalance arises because local priority effects lock in asymmetries in range size between species generated during speciation. In particular, when speciation involves the divergence of single populations (e.g. peripatry), priority effects lead to high phylogenetic imbalance because these rare lineages can persist over time but are less likely to diversify than the more widespread parental lineage (Fig. 4.3). In contrast, under vicariant speciation, in which species ranges are split symmetrically, priority effects instead result in trees that are highly balanced, with clade diversity more evenly distributed than expected under a pure-birth model (Fig. 4.5). Thus, our results show that local priority effects lead to high phylogenetic imbalance by re-enforcing pre-existing asymmetries in diversification rates, rather than generating these asymmetries in the first place.

Although the total number of species that could theoretically be packed into the metacommunity is constant across our models, local priority effects lead to a higher metacommunity richness at equilibrium, because rare species are more resistant to species extinction and can thus accumulate over time. In contrast, when invaders can displace residents, species endemic to a single site are at risk of being driven to extinction. Previous ecological studies have shown how priority effects can lead to stronger spatial turnover in species composition (Morton & Law 1997; Fukami & Morin 2003; Steiner & Leibold 2004), particularly when there is a diverse species pool, because of greater variability across sites in the order of species arrival (Chase 2010; Steiner 2014; Fukami 2015). Our macroevolutionary model highlights an alternative mechanism linking the strength of priority effects to species turnover and richness. Specifically, by reducing rates of species extinction, local priority effects lead to the greater persistence of rare species and the evolution of a more diverse species pool.

Our macroevolutionary model incorporating species diversification and niche evolution extends purely ecological models of local priority effects. The distinct signatures in phylogenetic tree shape and species ranges left by priority effects (Figs. 4.2, S4.4), provide potential candidate metrics to empirically evaluate the strength of priority effects in natural communities. We note that these signatures do not rest on our comparison between priority effects and deterministic displacement by invaders, as they are also evident when competitive outcomes are independent of arrival order. However, our model also makes a number of simplifications. For instance, we do not consider how selection at the level of individuals could drive the ecological divergence of local populations (i.e. character displacement) (Brown & Wilson 1956; Stroud *et al.* 2019) nor do we allow for increasing niche specialisation in response to competition. To some extent, our species-level model may capture the effects of selection for divergent niches, because species with similar ecological niches suffer greater extinction. Furthermore, while allowing individual level selection would likely allow a denser packing of the metacommunity as species can mutually adjust their niches, we do not expect that this would qualitatively alter our main conclusions.

Here we formulated a computational experiment that allows the effects of arrival order on competition to be manipulated, holding constant other factors such as the strength of competition and the ecological limit to diversity. While this allows us to identify the unique role of local priority effects in shaping macroevolutionary dynamics, our model is silent regarding the specific mechanisms that cause the competitive superiority, or indeed the equivalence, of residents or invaders. Yet, it is possible that different mechanisms could lead to contrasting dynamics. For instance, the strength of priority effects may vary with the relative population size of the invader and resident (Fukami 2015) or length of time they have been established (Svoboda *et al.* 2018). Equally, the success of invasive alien species has often been explained as a temporary fitness advantage (Hawkes 2007; Sheppard & Schurr 2019). However, whether this advantage dissipates because of a loss of fitness in the invader (e.g. natural enemies adapt to the invader), rather than an increase in fitness of the residents (e.g. residents adapt to the enemies carried by the invader), may have different implications for the resistance of the community to further invasions or the potential for the resident species to themselves become invaders at other sites. Here we purposefully bypassed the modelling of these ecological and demographic processes, but incorporating these features is an important avenue for future research (Aguilée *et al.* 2018).

## Conclusion

Our study represents a first attempt to integrate macroevolution into a metacommunity framework to test how local priority effects influence biodiversity dynamics. While our results suggest that certain macroevolutionary patterns—such as the enormous disparity in richness across clades—may be most consistent with the existence of strong priority effects operating within local communities, we find that local priority effects are not required to explain other classic features of adaptive radiations, including slowdowns in rates of diversification and the greater resistance of diverse regions to invasion. We show that even when local communities are governed by a constant turnover in composition driven by the continuous invasion of new species—as envisioned in Wilson's (1959) taxon cycle model—niche incumbency at the macroevolutionary scale arises as an emergent property of competitive pressure within the metacommunity.

## Chapter 5:

# General discussion

In this thesis I have examined how historical events over multiple spatial and temporal scales together with ecological interactions influence community composition, diversity and structure. The consequences of evolutionary history for community assembly have been studied from multiple angles before: from the exchange of biota between continents to the impact and order of community colonisation **(Chapter 1)**. However, these approaches have left important gaps in our understanding of how history impacts community assembly, because of three key shortcomings: (*i*) they focused on static patterns rather than using process-based approaches, (*ii*) focused on verbal theory that was extrapolated to larger temporal scales, and (*iii*) have not focused on how species accumulate in sympatry after speciation, i.e. how the regional species pool is assembled.

I proposed three questions in the introduction to further our understanding of how history impacts community assembly:

1. *How does the evolutionary history of clades shape the richness of ecological communities?* **(Chapter 2)**
2. *What is the order and timing of niche differentiation in the build-up of coexistence?* **(Chapter 3)**
3. *How do ecological interactions and evolutionary history interact in shaping communities?* **(Chapter 4)**

In the final part of the thesis I aim to synthesise the findings of the previous chapters and evaluate the role of evolutionary history in community assembly.

### Evolutionary history informs community assembly

In **(Chapter 2)**, I showed that evolutionary history, as captured by the reconstructed timing and sequence of speciation events in molecular phylogenies, can predict a significant proportion of variation in the maximum local diversity attained by different families of passerine birds. In particular, phylogenetic properties that result in long terminal branches, such as an early burst of speciation, increase the proportion of species in a clade that co-occur. This relationship arises because new species arise in allopatry, and so need time to expand their geographic ranges and accumulate in sympatry (Price 2008). In contrast, if speciation happened late in the radiation of a clade, most species will be young and still be in a state of allopatry, resulting in a lower proportion of species in sympatry. Differences in the evolutionary history of clades can thus result in substantial differences in the proportion of co-occurring species, even when the total diversity or age of clades are identical.

Although we were able to show that substantial variation in the proportion of sympatric species across clades is explained by evolutionary history, the extent to which this is a general pattern is unclear. The primary subject of **Chapters 2 and 3** have been Neotropical passerines. Passerines have been studied extensively in a historical context, such as the investigation of the riverine barriers that resulted in reproductive isolation and speciation (Naka & Brumfield 2018). These clades are primarily tropical, which may impact the conclusions given that the tropics have historically been more climatically stable compared to temperate regions which experience stronger climate fluctuations both across seasons and over longer temporal scales, such as glacial and interglacial events during the Quaternary. These climate fluctuations are likely to have resulted in species geographic ranges that are more dynamic over shorter time-scales, potentially erasing any signal of historical speciation patterns on current species distributions. The possibility that rapid range shifts may override the effects of deeper evolutionary history may also characterise highly mobile marine organisms. For instance, the persistence of habitat patches during the Quaternary were essential for reef fishes to survive, and 62% of variation in current day fish diversity is explained by the distance to these refugia (Pellissier *et al.* 2014). This illustrates that the evolutionary history of speciation may not limit colonisation times, as these can instead be constrained by time since disturbance events. Therefore, opportunities for colonisation of a community and the time since speciation could be decoupled across systems experiencing larger and more frequent disturbance events.

While simple metrics of phylogenetic structure (e.g. the mean phylogenetic distance between species) (Pigot & Etienne 2015) and richness can be reasonably predicted **(Chapter 2)** by the evolutionary history of a clade, predicting the precise species composition may be substantially more difficult. This is because multiple combinations of species may lead to the same diversity or phylogenetic structure and the particular combination of species may be inherently stochastic. For example, if we consider sister species that have recently arisen in allopatry, then given a particular colonisation rate we can predict whether only one species or both species are likely to be locally present at a given time following speciation. However, we would not be able to predict which sister species is present or absent from a simple time based model as all species are assumed to be governed by identical dynamics and thus composition is inherently stochastic. The number of possible combinations of species that could co-occur increases with clade size, and while clade history makes certain combinations more or less probable, additional information such as the geographic distance of species to the local community, the nature of geographic barriers and species intrinsic traits, are likely needed to improve predictability of community composition.

Previous studies have shown that a key limitation in the build-up of sympatry between sister species of passerine birds is competition for ecological resources. In particular, the probability of sympatry between species is elevated by divergence in ecomorphological traits related to resource use, especially the size and shape of the beak (Pigot & Tobias 2013; Pigot *et al.* 2018). Species which fail to diverge in these traits tend to remain in a persistent state of allopatry or parapatry for millions of year following their initial splitting. The models in **Chapter 2** do not incorporate or test the various factors that can facilitate or delay the attainment sympatry, but show that regardless of the mechanism, the build-up of sympatry within clades is highly protracted and that this an important constraint on total sympatric diversity, not just sister species co-occurrence. Together, these findings at both the level of sister species and clades raises an important outstanding question: If ecological niche divergence is often required for the attainment of sympatry in birds, when do these niche differences arise? One possibility is that niche differentiation may occur independently in allopatry and only species which happen to diverge in their niche can coexist when species come back into contact (Cadena 2007). Alternatively, niche differences could be driven by the process of species coming back into secondary contact, if competition drives displacement in resource or habitat use (Diamond 1973; Terborgh & Weske 1975). Resolving this question would provide additional insights into what delays the build-up of sympatry and how ecology and history interact to shape the assembly of biological communities.

### The timing of niche differentiation may explain the build-up of tropical diversity

In **Chapter 3**, I investigated how biological communities on tropical mountains have attained their incredible diversity, both in terms of the significant turnover of species along elevational gradients and the high levels of alpha diversity at any given altitude. I developed a framework based on Multistate Markov models and applied this to infer the relative order of elevational and geographical shifts in the distribution of Neotropical oscine and suboscine sister species. I showed that elevational turnover between sister species is explained by both sorting (change in elevation prior to establishing sympatry) and displacement (change in elevation upon establishing sympatry) and that these have occurred with relatively equal frequencies. That elevational displacement and sorting both leave a clear signature in the current distribution of species moves beyond a simplistic binary view of communities assembled by either one process or another, to show that a mix of different historical processes simultaneously operate in the assembly of communities.

I further showed that contrary to predictions of existing models of how communities are assembled on mountain slopes, most locally co-occurring species (i.e. occurring at the same elevation on the same mountain slope) arrived at this state without differentiation and subsequent convergence in elevational range. This shorter route to co-occurrence may explain why tropical mountain ranges are so species rich. Instead of long trajectories in which elevational differentiation is required for establishing secondary sympatry, sympatry is attained primarily without differentiating in elevation. These results demonstrate how a historical and temporal framework, is essential in understanding how species diversity has built-up over time and can shed new light on the causes of tropical mega-diversity.

While these results disentangle the relative frequency of different trajectories leading to co-occurrence and turnover on mountain slopes, they do not reveal the actual ecological processes that facilitate or limit co-occurrence, and in particular the role of divergence along additional niche dimensions beyond those associated with changes in elevation. For example, previous studies of neotropical avian sister species found that the attainment of secondary sympatry was limited by differentiation in beak and body size, consistent with the idea that strong inter-specific competition for ecological resources and micro-habitats prevents co-occurrence (Pigot *et al.* 2018). However, these results only applied for sister pairs where both sisters shared the same elevation range or broad habitat type. For species that occurred in different habitats, and thus where individuals do not frequently come into contact, resource related traits did not predict the attainment of sympatry (Pigot & Tobias 2013). An important next step is therefore to extend the models to incorporate multiple niche dimensions including both elevation and traits associated with resource and micro-habitat use.

Given the focus on elevation, an important question not addressed in **Chapter 3** is whether there is a predictable order in which different niche axes such as elevation, body size and microhabitat differentiate and are potentially saturated during radiations. For example, a predictable order of differentiation in which niche axes associated with body size get filled early in radiations, and differentiation of species across elevation occurs latter, has been described numerous times (Diamond 1986; Richman & Price 1992; Streelman & Danley 2003). In **Chapter 3**, we show that sister species of equivalent ages have attained sympatry through multiple different historical routes that either do or do not involve elevational differentiation. This might suggest that there is not a strict order in which niches differentiate, but that it is contingent on both ecological and environmental conditions, and species-specific factors such as genetic variation. Alternatively, it is possible that the different historical routes to sympatry taken by sister species may be predictable by the age of the radiations in which they occur, a hypothesis that could readily be tested using the models developed here.

While my results show that different sister species variously undergo sorting, displacement and retain conserved elevation ranges, they do not provide insight into what causes this variation in historical routes. It is possible that historical contingency could play an important role in determining which pathway a given sister pair will take making community assembly inherently unpredictable. For example, character displacement has been shown to result in stable coexistence between species of *Anolis* lizards (Stroud *et al.* 2019). Stroud et al. (2019) found that upon secondary contact of the Antiguan anole (*A. leachii*) and the Barbadian anole (*A. extremus*), only *leachii* underwent rapid character displacement, enabling it to expand into the range of *extremus*, while *extremus* failed to reciprocally expand its range. In this case, priority effects may have initially limited range expansion for both species, but it is unclear why only *leachii* evolved to overcome these constraints. Therefore, how initial historically contingent conditions can impact evolutionary trajectories is a key area requiring further work.

Together, **Chapters 2 and 3** show that current patterns of sympatric diversity within clades is strongly constrained by the timing of historical speciation and niche divergence events. However, these findings both represent major simplifications of reality because they treat phylogenetic history as a constraint that can influence community assembly, but ignore how the interactions occurring within communities can feed back to alter the dynamics of diversification (Mittelbach & Schemske 2015). Niche divergence and geographic range expansions become increasingly inhibited as ecological niche space within local communities becomes progressively filled. This has long been argued to be the key to understanding how ecological limits may operate to regulate the speciation and extinction dynamics of radiations at regional and global scales (Price *et al.* 2014). Determining the expected effects of these reciprocal feedbacks between scales thus emerges as a major unresolved question from **Chapters 2 and 3**.

### Various ecological interactions may have a deterministic impact on evolutionary history

In **chapter 4**, I developed a simulation model to address this gap in which both competitive interactions among species within local sites and the macroevolutionary diversification dynamics of species are incorporated. As expected, limits to the packing and volume of niche space at local (i.e. site) scales leads to an equilibrium diversity emerging at the regional scale (Rabosky & Hurlbert 2015). However, I also found that the assumptions made on how species arrival order at a site influences the outcome of competitive interactions can determine both local and global diversity dynamics. Under priority effects, species that arrived first are favoured and the persistence of rare species is promoted, which leads to higher overall clade diversity at equilibrium than when invaders are able to locally displace residents. In addition, this diversity is distributed unevenly across lineages as those lineages that arose or arrived first have more chances to speciate. Yet, I also found that a pattern of diversification consistent with 'niche incumbency' occurs independently of how arrival order structures competitive dynamics and thus regardless of the existence of local priority effects. Specifically, the rate at which new species arise and manage to colonise the metacommunity declines over time as species richness increases because of the increased intensity of competition (Walker & Valentine 1984; Alroy 1996), but this occurs even though niches are not filled in the sense that residents can theoretically always be displaced by invaders. Concomitantly, historical contingency caused by priority effects can both have lasting impacts on community composition, structure and diversity, but at the same time not influence deterministic outcomes such as niche incumbency at larger scales.

In the model, the importance of the order of arrival is simplistically envisioned in three distinct ways **(Chapter 4)**, whereby residents are always competitively superior, equivalent, or inferior to an invader regardless of when the resident arrived. However, the relative timing of arrival (not just the order) is likely to matter for priority effects in an empirical context (Chase 2003; Fukami 2015). Specifically, if species B arrives soon after the initial establishment of species A, species A may not have attained a high enough population density to pre-empt the available resources. This means that species B would be able to colonise the community regardless of arrival order. Therefore, the occurrence of priority effects will depend on population growth rates relative to arrival order, or other factors that might influence the timing of arrival between species. Investigating how these factors influences the generality and conditions under which priority effects impact macroevolutionary dynamics is an important avenue for future research.

A key finding of this study was that the existence of priority effects (i.e. arrival order), not just ecological limits to niche space, can profoundly shape the dynamics of species diversification and thus community structure and richness. It is therefore important to consider under what conditions priority effects that lead to stable variation in composition between communities are most likely to occur (Fukami 2015). At least three factors have previously been highlighted as important in ecological settings. First, there will need to be species present in the regional species pool that share substantial niche overlap and cannot coexist. If no species with substantial overlap are present, alternative community states cannot occur, and arrival order does not impact community assembly. Second, dispersal ability will need to be similar between species. If species A colonises the local community faster than B every time, there will be no variation in arrival order. While this may result in a priority effect in favour of A, community assembly becomes largely deterministic and creates no variation in composition. Third, it has been argued that for priority effects to be maintained the dynamics of species' abundances and range sizes within regional pools should be sufficiently decoupled from the local community dynamics (Fukami 2005, 2010). For instance, in an island-mainland model the island is dependent on the mainland, but the island likely does not contribute to diversity changes on the mainland (MacArthur & Wilson 1967). In contrast, in a strongly coupled metacommunity, if in some communities species A instead of species B starts to establish purely by chance, this will likely favour the further spread of species A due to a numerical advantage (Shurin *et al.* 2004). If metacommunity extinction rates are rapid, one competitor per niche may eventually remain and limit priority effects.

My results based on a dynamic evolutionary model show that when new species are constantly added through speciation, this can overcome the requirement for decoupling between local and regional dynamics (Shurin *et al.* 2004; Fukami 2015). Specifically, newly originating species can replace those that have gone extinct and while the species that experience priority effects might be shifting over time, priority effects and historical contingency in community assembly can persist. The evolutionary models also show that although species can evolve to have non-overlapping niches and thus eliminate competition and priority effects, the formation of new species which initially have similar niches to their ancestor (or sister lineage) renews the action of priority effects. This phenomenon is further enhanced when ecological niche space and thus niche divergence is limited. In this case, even distantly related species may be subject to priority effects as they conserve or converge on similar niches.

While my model highlights the importance of an evolutionary perspective, further work is needed to fully understand these dynamics. For example, the model assumes identical dispersal abilities among species and thus does not address the importance of differences in vagility for priority effects, or in turn, how priority effects may influence the evolution of dispersal ability. In addition, while our results in **Chapter 3** show that niche divergence on secondary contact is an important facilitator of local co-occurrence, this was not considered in our priority effects model where co-occurrence at a site instead depends only on ecological sorting. While niche displacement could enable species to escape from priority effects early in species radiations, if ecological niche space is limited, I expect such displacements to become progressively more difficult as species richness increases, leading to priority effects strengthening over time.

The issue of how a species pool arises that supports priority effects lays bare a larger theme that this thesis has tried to address. This encompasses both the application of verbal ecological theory to macroevolutionary scales **(Chapter 4)**, and ecological studies ignoring the macroevolutionary processes that have shaped phylogenetic trees **(Chapter 2)**. The key issue here is that the same patterns have often been interpreted from the point of view of processes that act on vastly different temporal and spatial scales. For instance, patterns of phylogenetic overdispersion and clustering were often interpreted as extensions of Modern Coexistence Theory (MCT) (Chesson 2000; Mayfield & Levine 2010). Here, overdispersion may be an indication of niche differences being favoured for stable coexistence, while clustering might indicate either environmental filtering or equalisation of competitive abilities among community members. However, it is still an open question whether clustering and overdispersion should be expected to arise over the evolutionary history of clades under the framework proposed by Mayfield and Levine (2010). This is because MCT has not been extended to incorporate diversification dynamics (Pastore *et al.* 2021; Yamamichi *et al.* 2022) and because allopatric speciation alone can result in the same patterns in absence of competition (Pigot & Etienne 2015). Considering how species arose in the first place can therefore lead to new insight about how important ecological processes are in shaping community assembly.

### The predictability of community ecology in the light of history

Stephen J Gould argued for the importance of chance and historical contingency in shaping the evolution of life on Earth. According to Gould, the appearance of directionality and progress in the fossil record were at most the outcome of passive changes (Gould 1996), with the sequential replacement of taxonomic groups occurring due to stochastic variation in survival rather than a result of adaptive superiority (Gould & Calloway 1980). The view that evolutionary history is stochastic and unpredictable has also pervaded community ecology. This was epitomised at the end of the 20th century with Lawton's (1999) claim that community ecology is a 'mess' and devoid of any meaningful laws.

While many have since argued against Lawton's view (McGill *et al.* 2006), history with its contingent and stochastic nature is still generally seen as an important source of the 'mess' in community ecology. The results of this thesis question this view, highlighting both how historically contingent processes do not always lead to unpredictable patterns and that history can even generate order in community structure and diversity. For example, while priority effects might lead to unpredictable variation in local community composition, I found that this does not alter the temporal dynamics of species diversification **(Chapter 4)**. This suggests that historical contingency arising at one scale (the local community) does not mean that larger scale patterns (the regional pool) will also be unpredictable. At the same time, I found that while competition for limited resources means that the temporal dynamics of diversification unfold in the same way regardless of the existence of priority effects, there is substantial stochasticity in the identity of the species that become the dominant lineages. Therefore, while some patterns like phylogenetic imbalance are expected to be strongly shaped by local historical contingency, other patterns are expected to be more predictable and less influenced by stochasticity at local scales. Determining when historical contingency at local scales matters at larger scales is an area ripe for further investigation.

Viewed from the opposite perspective, the finding that variation in local diversity can be predicted from the timing of speciation events within clades, suggests that the predictability of community patterns ultimately depends on the predictability in the macroevolutionary dynamics of speciation and lineage persistence. While the timing of individual speciation events may be inherently unpredictable due to the nature of geographic barriers and random mutations (Pigot *et al.* 2010), to the extent that variation in rates of speciation across clades and geographic space are predictable on the basis of the intrinsic properties of organisms (Miller *et al.* 2022; Yamaguchi 2022) and environmental conditions (Weir & Schluter 2007), this implies that these factors will also indirectly lead to predictable variation in community structure and diversity.

This thesis shows how combining phylogenetic data on the timing of these historical events and macroevolutionary dynamics with process-based models can shed new light on how the evolutionary history of lineages and their interactions shape community assembly. History might act over various scales and in various ways, but its outcome is not always stochastic and unpredictable. My results show that community patterns often explained in terms of environmentally determined limits to coexistence, may instead arise from historical factors alone. This suggests that evolutionary history could have a much greater impact on present-day community patterns than is usually appreciated and argue for a re-appraisal of the way we view the consequences of history for community and macroecology. Rather that history being a source of statistical noise, generating inconvenient anomalies and deviations around the neat, predictable patterns expected from environmental determinism, evolutionary history will provide a central component in a predictive science of community ecology and in the macroecology of coexistence.

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# Appendices

## Appendix 1: Supplementary material Chapter 2

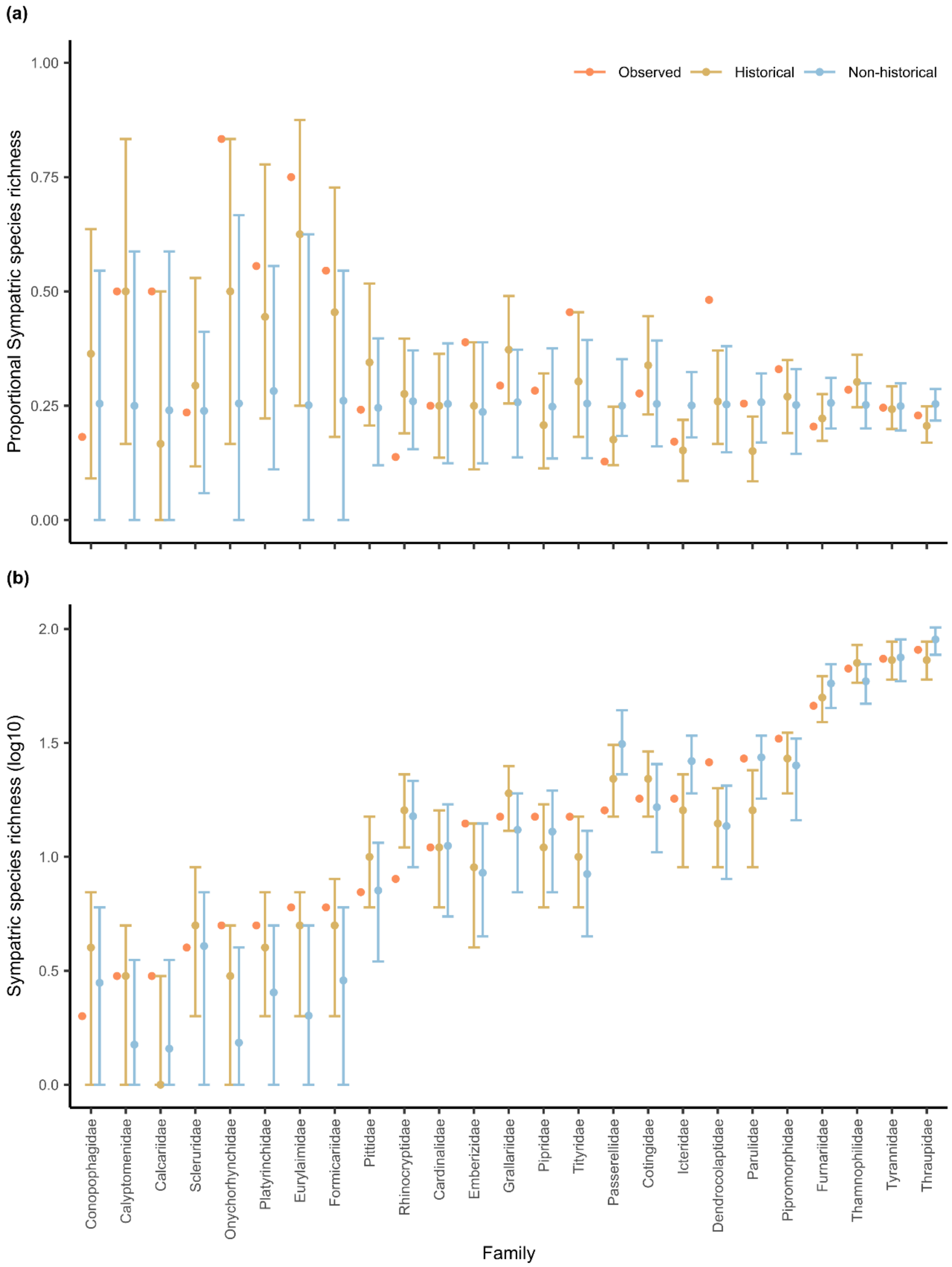

**Figure S2.1** Observed and predicted richness of passerine clades. a) shows the proportional maximum sympatric diversity, whereas b) shows the absolute maximum diversity. The empirical (orange) data points show the maximum richness of the clades found across 24 km$^2$ grid cells. Predictions for the historical model under the colonisation rate recovered by DAMOCLES (yellow) are shown, and simulations under the non-historical model are shown in blue. Bars represent the 95% confidence intervals of the richness of the community recovered under 100 simulations for each null model. For the historical model 22 out of 25 empirical richness values fall within the 95% CI, and for the non-historical model 16 out of 25.

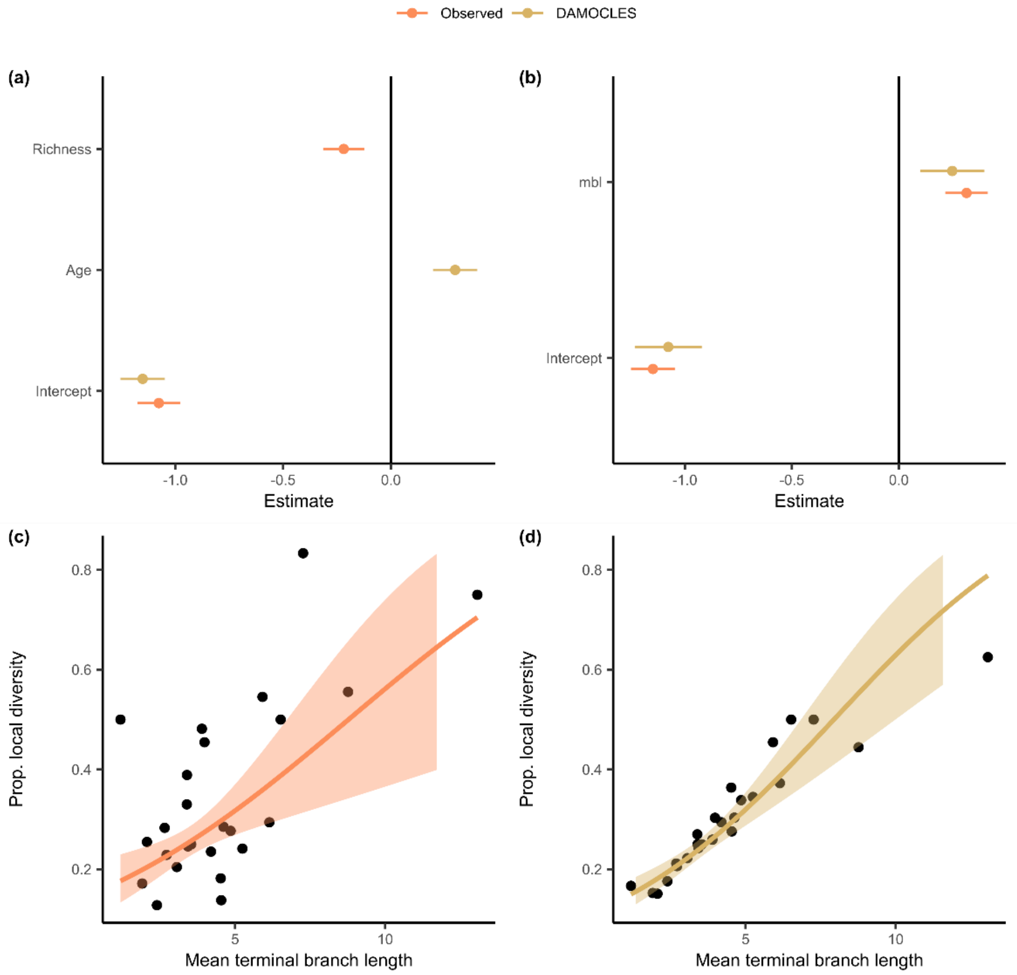

**Figure S2.2** Relationship between evolutionary history and proportional sympatric diversity (24 km$^2$). Colours denote the empirical relationships for all clades (orange) and relationships simulated under DAMOCLES are shown in yellow. (a) Minimum adequate models (MAMs) for the explanatory variables where mean terminal branch length had not been added are shown. Non-significant variables are not shown. (b) MAMs for models including mean terminal branch length (mbl). GLM Input data was scaled and mean-centred for visualisation, and bars represent 95%CI's. Predicted relationship between mbl and the maximum proportion of species in sympatry for the (c) empirical and (d) simulated data. Shaded areas indicate 95% CI's, dots represent the empirical and simulated data, and the coloured lines show the fitted relationships.

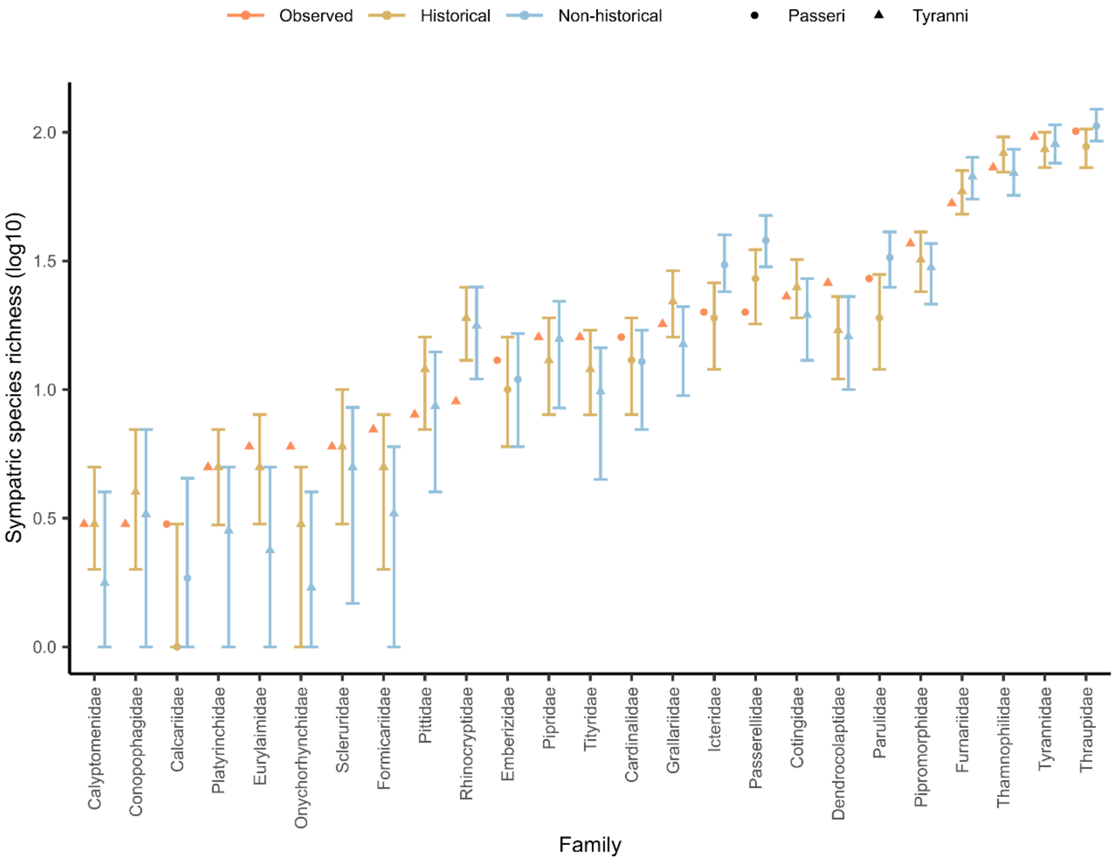

**Figure S2.3** Observed and predicted absolute sympatric richness of passerine clades. The empirical (orange) data points show the maximum richness of the clades across all 96 km$^2$ grid cells that they occupy. Predictions for the historical model under the colonisation rate recovered by DAMOCLES (yellow) and the non-historical null model are shown. Bars represent the 95% confidence intervals of the richness of the community recovered under 1000 simulations. For the respectively the historical and non-historical model 22 out of 25 and 15 out of 25 empirical proportions fall within the 95% CI.

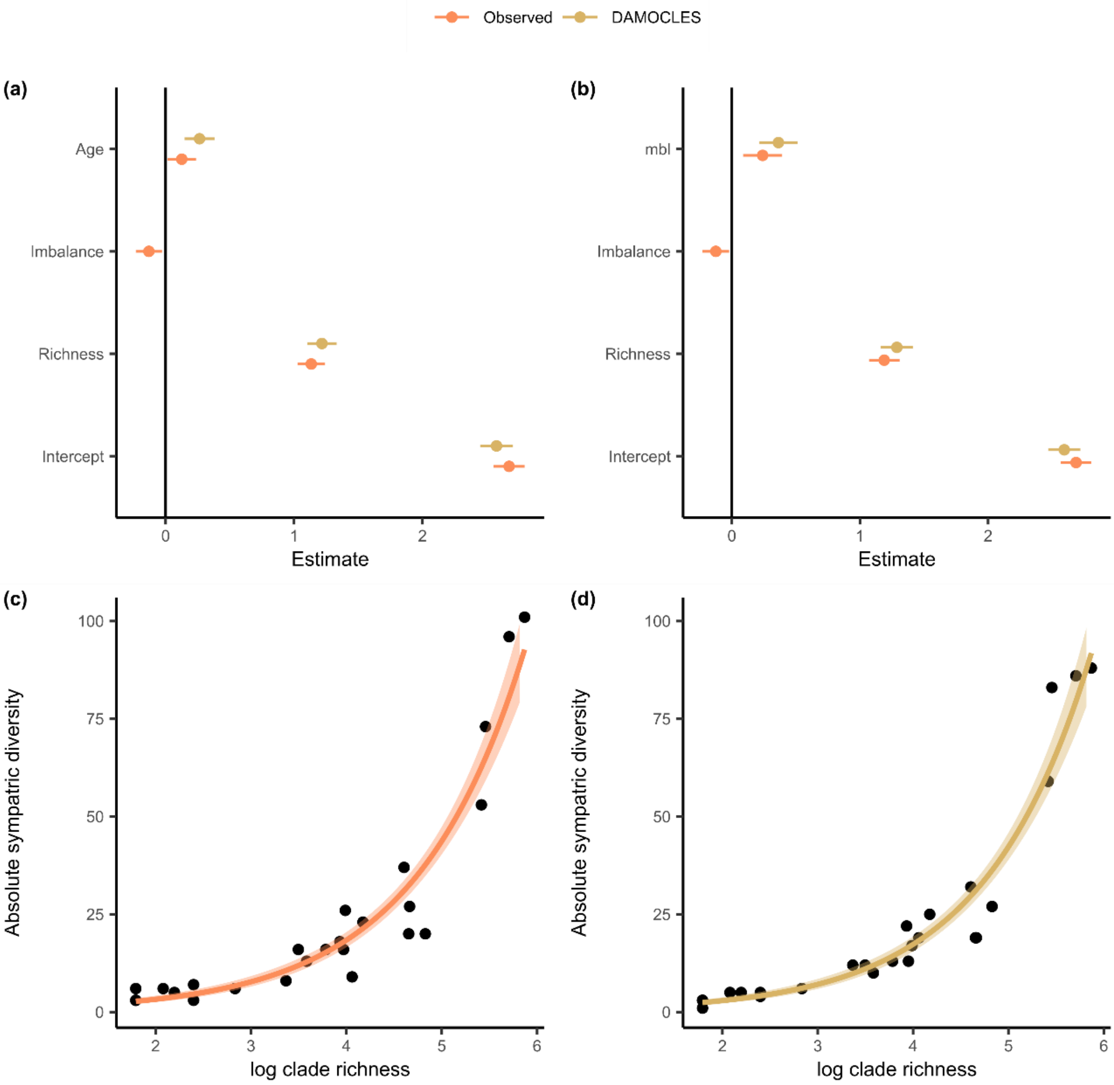

**Figure S2.4** Relationship between evolutionary history and absolute sympatric diversity. Colours denote the empirical relationships for all clades (orange) and relationships simulated under DAMOCLES are shown in yellow. (a) Minimum adequate models (MAMs) for the explanatory variables where mean terminal branch length had not been added are shown. Non-significant variables are not shown. (b) MAMs for models including mean terminal branch length (mbl). GLM Input data was scaled and mean-centred for visualisation, and bars represent 95% CI's. Predicted relationship between log-clade richness and absolute sympatric diversity for the (c) empirical and (d) simulated data. Dots represent the empirical and simulated data respectively, whereas the shaded area and coloured line show the fitted MAM and 95% CI's.

## Appendix 2: Supplementary material Chapter 3

### *Analysis data Freeman 2015*

Additional to the dataset analysed in the main text, we analysed a previously compiled dataset consisting of avian sister species resident in tropical mountain ranges in the

Neotropics, New Guinea, or the Himalayas (Freeman 2015) (n = 182). Briefly, the dataset contained information on the divergence of elevational ranges, geographical overlap, and the genetic distance between pairs. Elevational data was compiled from the existing literature and field guides at the range-wide level. Geographic overlap was scored categorically and according to pairs being either allopatric or sympatric. Sister species were selected by performing a survey of published molecular phylogenies that at least had sampled 80% of species per genus. Sympatry was defined as species that were present along the same mountain slope. This meant that geographical overlap could range from being widespread or minimal if the species were elevational replacements. In contrast, allopatric pairs occurred on distinct mountain ranges. Lastly, genetic distance was derived from homologous mitochondrial DNA sequences. Rates of mitochondrial evolution appear highly conserved in birds with an approximate rate of ~2% per million-year interval (Weir & Schluter 2008). Based on this assumption, the divergence between sequences was calculated and subsequently divided by 0.02, giving a more meaningful interpretation of when species diverged from their most recent common ancestor.

With this dataset we performed the same set of analyses as for the main paper. We first delineated in which state species occurred depending on if they were sympatric or allopatric, if they shared elevational ranges (20% threshold) or not, and if they showed differentiation in sympatry but not in allopatry. Thirteen pairs had previously been identified by Freeman (2015) that likely showed a degree of differentiation in sympatry but not in allopatry (state 2). As for the sister species in the main text, we utilised field guides and HBW to quantify any regional intraspecific variation in elevational ranges in sympatry compared to allopatry for these species. We did not quantify regional elevational differentiation across all sympatric pairs as we did in the main analysis. This resulted in five out of thirteen matching the conditions of having <20% overlap in sympatry and >20% in allopatry. Overall, we found that 52% of species were allopatric while overlapping in elevation (state 1), 3% of pairs diverged in elevation in sympatry but showed overlap in allopatry (state 2), 2% of pairs were allopatric but showed elevational differentiation (state 3), 14% of pairs were sympatric and showed no elevational overlap (state 4), and 29% of pairs were sympatric and showed substantial elevational overlap (state 5). Meeting our assumptions of allopatric speciation, species in state 1 appear to be the youngest (2.56 Myr) compared to all other states (state 2 = 3.79, state 3 = 2.89, state 4 = 4.20, and state 5 = 3.57 Myr).

We fitted the same continuous time multi-state Markov models to the data via maximum likelihood to estimate the transition rates between states, the prevalence of states through time, and the trajectories taken by sister species. These models again had a maximum of seven parameters corresponding to the seven possible transitions between states (Figure 3.1). Model fit was compared across all 877 models according to AIC, and we report the results of the model-averaged parameter values of all highly supported models (ΔAIC ≤ 2 of best model). Using the model-averaged parameter estimates, we performed posterior-predictive simulations to calculate the relative frequency of the trajectories taken, how elevational replacements originated, and how much trajectories contributed to sympatric, co-occurring alpha diversity (Figure S3.2).

Additional simulations were performed to evaluate how well our model would be able to predict the transition rates. Six scenarios are simulated via a Gillespie algorithm, prior to fitting the Markov models to test how well the simulated parameters are recovered (see Methods). Although our modelling framework remains intact independent of dataset, the underlying dataset may have an impact on accuracy and bias in inference. Specifically, differences in the age distribution of sister species could be skewed in different directions, e.g. fewer or more older species pairs could influence estimation. However, we show that results for both datasets in terms of empirical patterns (Figure S3.2), recovered rates, and the assessment of accuracy and bias is qualitatively similar (Table S3.3, S3.4), and accurate for the early transition rates.

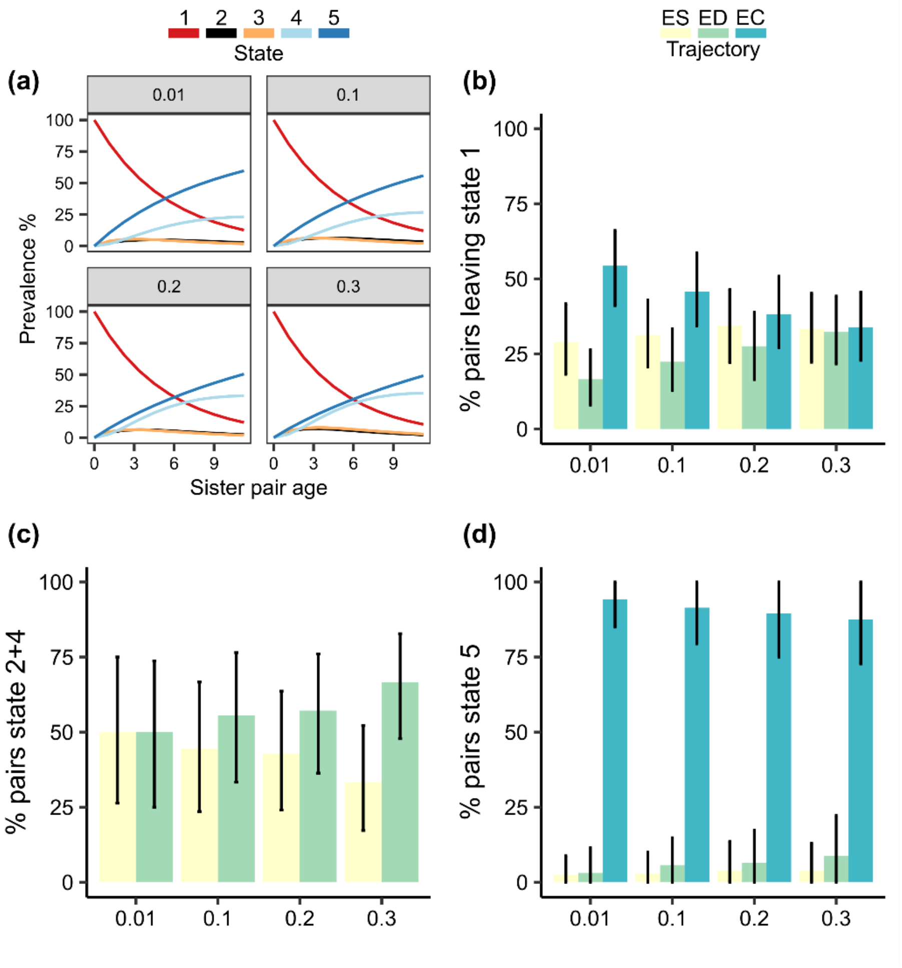

**Figure S3.1** Frequency of trajectories taken to sympatry in relation to the elevational overlap threshold. a) prevalence of states through time for four thresholds below which sister species are considered to be non-overlapping in elevation. States follow the same legend colour scheme as Figure 1 and 2. b) Percentage of pairs that transitioned to respectively state 3 (yellow; ES), state 2 (green; ED), or state 5 (blue; EC) from the ancestral state. c) Percentage of pairs that have reached sympatry but do not overlap in elevation, i.e. elevational replacements, through respectively ES (yellow) and ED (green). d) Percentage of pairs that are currently sympatric with overlapping ranges and have reached this state through respectively ES, ED, and EC. For b), c), and d) the x-axis shows the elevational thresholds.

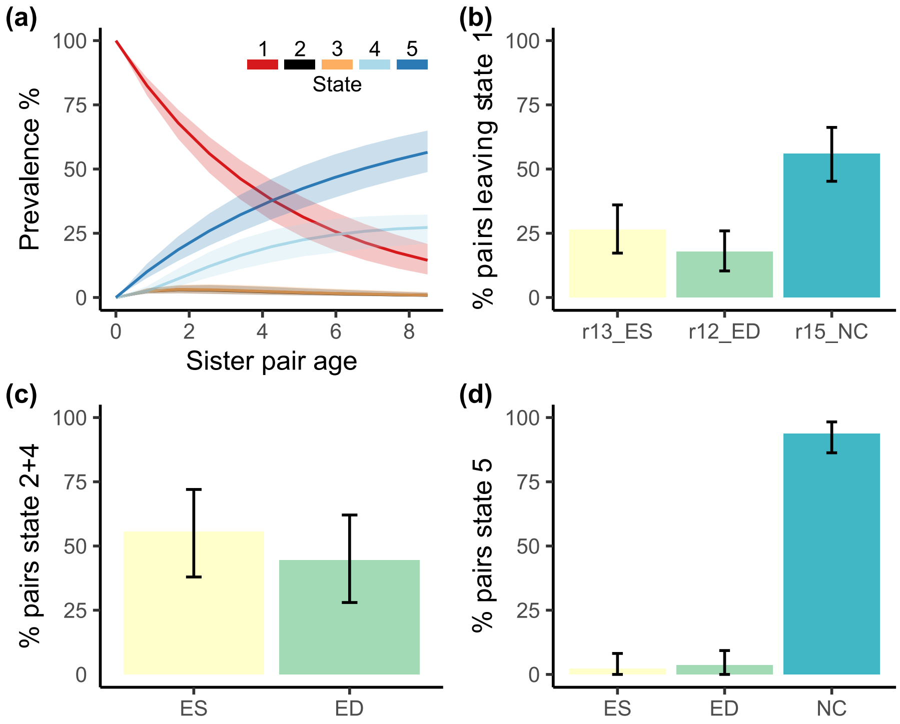

**Figure S3.2** Sister pair predicted prevalence and trajectories taken using the Freeman 2015 dataset. a) prevalence of the five states that are shown in Figure 1 through time as predicted by the model with the lowest AIC. Shaded areas correspond to the 95%CI of each state. b) percentage of pairs that have left the ancestral state of allopatry and overlapping elevational ranges. r13 corresponds to differentiation in elevation while allopatric, r12 represents differentiation in elevation on secondary contact, and r15 represent direct transition to sympatry conserving elevational ranges. c) bars represent the proportion of pairs that are currently in sympatry with non-overlapping elevation, i.e. elevational replacements, and if they experienced Elevational sorting (ES) or Elevational displacement (ED) to attain this state. d) percentage of pairs that have reached sympatry with overlapping elevational ranges through each route.

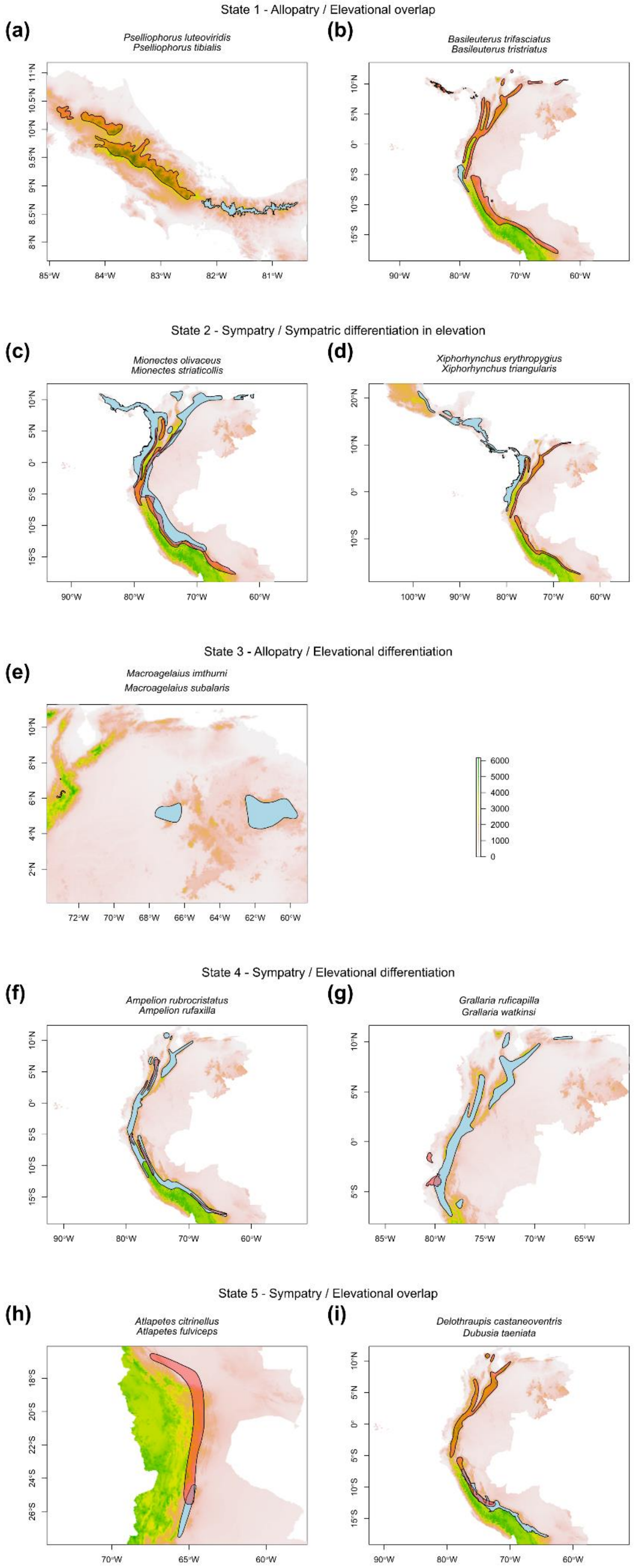
State 1 - Allopatry / Elevational overlap
(a)
Pselliophorus luteoviridis
Pselliophorus tibialis
11°N
10.5°N
10°N
9.5°N
9°N
8.5°N
8°N
85°W
84°W
83°W
82°W
81°W
(b)
Basileuterus trifasciatus
Basileuterus tristriatus
10°N
5°N
0°
5°S
10°S
15°S
90°W
80°W
70°W
60°W
State 2 - Sympatry / Sympatric differentiation in elevation
(c)
Mionectes olivaceus
Mionectes striaticollis
10°N
5°N
0°
5°S
10°S
15°S
90°W
80°W
70°W
60°W
(d)
Xiphorhynchus erythropygius
Xiphorhynchus triangularis
20°N
10°N
0°
10°S
100°W
90°W
80°W
70°W
60°W
State 3 - Allopatry / Elevational differentiation
(e)
Macroagelaius imthurni
Macroagelaius subalaris
10°N
8°N
6°N
4°N
2°N
72°W
70°W
68°W
66°W
64°W
62°W
60°W
6000
5000
4000
3000
2000
1000
0
State 4 - Sympatry / Elevational differentiation
(f)
Ampelion rubrocristatus
Ampelion rufaxilla
10°N
5°N
0°
5°S
10°S
15°S
90°W
80°W
70°W
60°W
(g)
Grallaria ruficapilla
Grallaria watkinsi
10°N
5°N
0°
5°S
85°W
80°W
75°W
70°W
65°W
State 5 - Sympatry / Elevational overlap
(h)
Atlapetes citrinellus
Atlapetes fulviceps
18°S
20°S
22°S
24°S
26°S
70°W
65°W
60°W
(i)
Delothraupis castaneoventris
Dubusia taeniata
10°N
5°N
0°
5°S
10°S
15°S
90°W
80°W
70°W
60°W

**Figure S3.3** Patterns of sympatry and allopatry in montane birds. Each of the five states shown in figure 1 are represented by empirical range maps of sister pairs contained in our analysis. (a) and (b) show examples of allopatric sister species where species have not differentiated in elevational range (state 1). (c) and (d) show cases where sister species only differentiate in elevation while sympatric (state 2), and (e) shows a case where elevational differentiation has occurred prior to attaining sympatry (state 3). (f) and (g) respectively contain sisters that are sympatric and have divergent elevations, but the degree of geographical overlap varies significantly (state 4). (h) and (i) show that sisters may be sympatric without having differentiated in elevation for both long and short stretches (state 5). Range maps were obtained from Birdlife International and elevational data was obtained from Natural Earth at a 1:110m scale.

### *Accuracy and reliability*

In order to assess the accuracy and precision of the model in recovering the transition rates we assessed five separate scenarios. Scenarios S1 to S3 refer to respectively cases where >80% of the sister pairs that leave the initial state of allopatry with no elevational differentiation go through respectively elevational (S1) sorting, (S2) displacement or (S3) conservatism. For scenario S4 we model an equal rate scenario to investigate if there is any bias in overestimating any particular rate. Lastly, for S5 we test how well we can recover the true rates from a scenario where we simulate under the empirical model estimates. These scenarios were chosen to be reflective and fair comparisons to our empirical estimates, and to uncover if any trajectory through the five states was preferred over the others. The order-of-magnitude in rate variation is of a similar level compared to the variation in rates uncovered for the empirical model estimates, and for S4 the transition rate of 0.05 was chosen as it is comparable to the initial rates of the empirical model estimates. In contrast, if the initial rates in our simulated scenarios would be higher, e.g. r12 = 0.25, this would lead to more accurate and precise estimates for the latter rates, e.g. r24 and r25, but would not be reflective of the initial rates that were estimated. Our accuracy and reliability analyses can therefore be seen as conservative in the ability of the model to infer transition rates.

**Table S3.1** Estimates of simulated transition rates derived from the model-averaged approach. For each scenario 100 datasets were simulated forward into time under the true rates where species pair ages were retained relative to the empirical data. Species pairs could transition between states until the simulation reached the pair's age. Subsequently, Markov models were fitted to mimic the empirical analysis in order to estimate transition rates (r12, r13, r15, r24, r25, r34, r45,). The first three scenarios (S1, S2, & S3) represent scenarios where >80% of pairs go through elevational sorting, displacement and conservatism respectively. Under scenario S4 rates are equal among transitions to detect any particular bias and S5 represents how well rates are reconstructed from datasets simulated under the rates estimated for the empirical data. For each dataset model-averaged parameter values were obtained. Median and the 95%CI, between parentheses, were constructed per scenario from the estimates across these datasets.

| | **S1 - Elevational sorting** | | **S2 - Elev. displacement** | | **S3 - Elev. conservatism** | |
|---|---|---|---|---|---|---|
| | **True rate** | **Estimated** | **True rate** | **Estimated** | **True rate** | **Estimated** |
| **r12** | 0.01 | 0.01 (0-0.03) | 0.1 | 0.09 (0.07-0.14) | 0.01 | 0.01 (0.01-0.08) |
| **r13** | 0.1 | 0.1 (0.07-0.13) | 0.01 | 0.01 (0-0.03) | 0.01 | 0.01 (0-0.02) |
| **r15** | 0.01 | 0.01 (0-0.02) | 0.01 | 0.01 (0-0.02) | 0.1 | 0.09 (0.04-0.13) |
| **r24** | 0.01 | 0.07 (0.02-0.88) | 0.1 | 0.09 (0.02-0.29) | 0.01 | 0.07 (0.03-2.22) |
| **r25** | 0.01 | 0.05 (0.02-0.22) | 0.1 | 0.07 (0.01-0.18) | 0.01 | 0.06 (0.02-1.59) |
| **r34** | 0.1 | 0.09 (0.01-0.21) | 0.01 | 0.07 (0.02-0.41) | 0.01 | 0.08 (0.03-1.23) |
| **r45** | 0.1 | 0.05 (0.01-0.35) | 0.01 | 0.06 (0.02-0.31) | 0.01 | 0.06 (0.03-2.54) |
| | **S4 – Equal rates** | | **S5 – Estimated rates** | | | |
| | **True rate** | **Estimated** | **True rate** | **Estimated** | | |
| **r12** | 0.05 | 0.05 (0.03-0.08) | 0.06 | 0.06 (0.03-0.11) | | |
| **r13** | 0.05 | 0.05 (0.03-0.08) | 0.06 | 0.07 (0.03-0.11) | | |
| **r15** | 0.05 | 0.05 (0.03-0.07) | 0.07 | 0.07 (0.03-0.09) | | |
| **r24** | 0.05 | 0.05 (0.01-0.13) | 0.32 | 0.27 (0.05-0.73) | | |
| **r25** | 0.05 | 0.05 (0.01-0.32) | 0.06 | 0.12 (0.04-0.52) | | |
| **r34** | 0.05 | 0.05 (0.02-0.22) | 0.53 | 0.54 (0.1-1.28) | | |
| **r45** | 0.05 | 0.06 (0.03-0.65) | 0.06 | 0.06 (0.03-0.39) | | |

**Table S3.2** Estimates of simulated transition rates derived from the 'best' model approach. For each of the 100 datasets per scenario this table represents the parameters estimated by the 'best' model. Median and the 95%CI, between parentheses, were constructed per scenario from the 'best' model estimates across these datasets. Additional, coverage is shown referring to the *n* cases out of 100 in which the confidence intervals of the estimates for the individual 'best' model capture the true rates. For details see Table S3.1.

| | **S1 - Elevational sorting** | | | **S2 - Elevational displacement** | | |
|---|---|---|---|---|---|---|
| | **True rate** | **Estimated** | **Coverage** | **True rate** | **Estimated** | **Coverage** |
| **r12** | 0.01 | 0.01 (0-0.03) | 82 | 0.1 | 0.1 (0.07-0.14) | 92 |
| **r13** | 0.1 | 0.1 (0.07-0.13) | 95 | 0.01 | 0.01 (0-0.02) | 85 |
| **r15** | 0.01 | 0.01 (0-0.02) | 91 | 0.01 | 0.01 (0-0.02) | 82 |
| **r24** | 0.01 | 0.07 (0-0.96) | 47 | 0.1 | 0.09 (0.01-0.28) | 71 |
| **r25** | 0.01 | 0.02 (0-0.13) | 50 | 0.1 | 0.09 (0-0.22) | 55 |
| **r34** | 0.1 | 0.1 (0.01-0.23) | 75 | 0.01 | 0.08 (0-0.77) | 41 |
| **r45** | 0.1 | 0.05 (0-0.54) | 42 | 0.01 | 0.02 (0-0.39) | 42 |
| | **S3 - Elevational conservatism** | | | **S4 – Equal rates** | | |
| | **True rate** | **Estimated** | **Coverage** | **True rate** | **Estimated** | **Coverage** |
| **r12** | 0.01 | 0.01 (0.01-0.11) | 79 | 0.05 | 0.05 (0.03-0.08) | 87 |
| **r13** | 0.01 | 0.01 (0-0.02) | 92 | 0.05 | 0.05 (0.03-0.08) | 83 |
| **r15** | 0.1 | 0.09 (0.01-0.13) | 82 | 0.05 | 0.05 (0.02-0.07) | 87 |
| **r24** | 0.01 | 0.08 (0.01-1.94) | 35 | 0.05 | 0.05 (0-0.16) | 91 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **r25** | 0.01 | 0.02 (0.01-3.35) | 55 | 0.05 | 0.05 (0-0.45) | 80 |
| **r34** | 0.01 | 0.09 (0.01-0.99) | 20 | 0.05 | 0.05 (0.01-0.22) | 80 |
| **r45** | 0.01 | 0.02 (0.01-3.35) | 54 | 0.05 | 0.05 (0.02-0.28) | 81 |

| | **S5 – Estimated rates** | | |
|---|---|---|---|
| | **True rate** | **Estimated** | **Coverage** |
| **r12** | 0.06 | 0.06 (0.02-0.1) | 72 |
| **r13** | 0.06 | 0.07 (0.03-0.11) | 81 |
| **r15** | 0.07 | 0.07 (0.01-0.1) | 86 |
| **r24** | 0.32 | 0.37 (0.02-0.76) | 64 |
| **r25** | 0.06 | 0.07 (0.02-0.77) | 58 |
| **r34** | 0.53 | 0.51 (0.05-1.46) | 81 |
| **r45** | 0.06 | 0.06 (0-0.48) | 67 |

**Table S3.3** Estimates of simulated transition rates for the Freeman dataset using the 'best' model approach. For each of the 100 datasets per scenario this table represents the parameters estimated by the 'best' model. Median and the 95%CI, between parentheses, were constructed per scenario from the 'best' model estimates across these datasets. For details see Table S3.1.

| | **S1 - Elevational sorting** | | **S2 - Elev. displacement** | | **S3 - Elev. conservatism** | |
|---|---|---|---|---|---|---|
| | **True rate** | **Estimated** | **True rate** | **Estimated** | **True rate** | **Estimated** |
| **r12** | 0.01 | 0.01 (0-0.04) | 0.10 | 0.1 (0.07-0.13) | 0.01 | 0.01 (0-0.07) |
| **r13** | 0.10 | 0.1 (0.07-0.13) | 0.01 | 0.01 (0-0.04) | 0.01 | 0.01 (0-0.03) |
| **r15** | 0.01 | 0.01 (0-0.02) | 0.01 | 0.01 (0-0.02) | 0.10 | 0.1 (0.03-0.12) |
| **r24** | 0.01 | 0.01 (0-0.47) | 0.10 | 0.1 (0-0.18) | 0.01 | 0.06 (0.01-0.68) |
| **r25** | 0.01 | 0.01 (0-0.12) | 0.10 | 0.02 (0-0.13) | 0.01 | 0.02 (0-2.03) |
| **r34** | 0.10 | 0.1 (0.01-0.18) | 0.01 | 0.08 (0-0.9) | 0.01 | 0.09 (0-0.9) |
| **r45** | 0.10 | 0.09 (0-0.46) | 0.01 | 0.08 (0-0.77) | 0.01 | 0.07 (0.01-4.38) |
| | **S4 – Equal rates** | | **S5 – Estimated rates** | | | |
| | **True rate** | **Estimated** | **True rate** | **Estimated** | | |
| **r12** | 0.05 | 0.05 (0.03-0.08) | 0.04 | 0.07 (0.01-0.15) | | |
| **r13** | 0.05 | 0.05 (0.03-0.08) | 0.06 | 0.07 (0-0.12) | | |
| **r15** | 0.05 | 0.05 (0.01-0.06) | 0.13 | 0.09 (0.03-0.16) | | |
| **r24** | 0.05 | 0.05 (0-0.12) | 0.66 | 0.86 (0.01-3.3) | | |
| **r25** | 0.05 | 0.05 (0.01-0.42) | 0.09 | 0.58 (0.01-2.66) | | |
| **r34** | 0.05 | 0.05 (0.01-0.22) | 1.31 | 1.18 (0.01-4.59) | | |
| **r45** | 0.05 | 0.05 (0.01-0.91) | 0.04 | 0.07 (0.01-0.37) | | |

**Table S3.4** Freeman dataset simulated transition rates estimated by the model-averaged approach. For each of the 100 datasets per scenario this table represents the parameters estimated via model-averaging. Median and the 95%CI, between parentheses, were constructed per scenario from the model-averaged estimates of every dataset. For details see Table S3.1.

| | **S1 - Elevational sorting** | | **S2 - Elev. displacement** | | **S3 - Elev. conservatism** | |
|---|---|---|---|---|---|---|
| | **True rate** | **Estimated** | **True rate** | **Estimated** | **True rate** | **Estimated** |

| | | | | | | |
|---|---|---|---|---|---|---|
| **r12** | 0.01 | 0.01 (0-0.03) | 0.10 | 0.1 (0.07-0.13) | 0.01 | 0.01 (0.01-0.05) |
| **r13** | 0.10 | 0.1 (0.06-0.13) | 0.01 | 0.01 (0-0.03) | 0.01 | 0.01 (0.01-0.02) |
| **r15** | 0.01 | 0.01 (0-0.02) | 0.01 | 0.01 (0-0.03) | 0.10 | 0.1 (0.05-0.12) |
| **r24** | 0.01 | 0.05 (0.02-0.36) | 0.10 | 0.09 (0.02-0.17) | 0.01 | 0.06 (0.02-1.01) |
| **r25** | 0.01 | 0.05 (0.02-0.14) | 0.10 | 0.03 (0.01-0.1) | 0.01 | 0.06 (0.02-1.24) |
| **r34** | 0.10 | 0.09 (0.03-0.14) | 0.01 | 0.07 (0.02-0.77) | 0.01 | 0.07 (0.03-0.71) |
| **r45** | 0.10 | 0.06 (0.01-0.33) | 0.01 | 0.05 (0.01-0.42) | 0.01 | 0.06 (0.03-3.54) |

| | **S4 – Equal rates** | | **S5 – Estimated rates** | |
|---|---|---|---|---|
| | **True rate** | **Estimated** | **True rate** | **Estimated** |
| **r12** | 0.05 | 0.05 (0.03-0.08) | 0.04 | 0.07 (0.02-0.13) |
| **r13** | 0.05 | 0.05 (0.03-0.07) | 0.06 | 0.06 (0.01-0.1) |
| **r15** | 0.05 | 0.05 (0.02-0.06) | 0.13 | 0.1 (0.06-0.16) |
| **r24** | 0.05 | 0.05 (0.02-0.1) | 0.66 | 0.62 (0.07-2.48) |
| **r25** | 0.05 | 0.05 (0.03-0.33) | 0.09 | 0.64 (0.06-2) |
| **r34** | 0.05 | 0.05 (0.02-0.18) | 1.31 | 1.25 (0.11-4.11) |
| **r45** | 0.05 | 0.05 (0.04-0.68) | 0.04 | 0.07 (0.02-0.28) |

### *How often do we correctly infer the trajectories taken?*

To estimate the frequency at which we correctly infer the prevalence of each trajectory, be it ES, ED, or ES, we again follow a multi-step approach. First, with the rates recovered for the empirical data, e.g. Table S3.1 scenario 5, we simulate 100 primary datasets for which we know the states that each sister pair will have passed through. Second, for each dataset we perform the same modelling procedures as for the empirical data to recover the transition rates – note step 1 and 2 are identical to recovering the rate estimates for Table S1. Third, using the rates recovered per dataset, we simulate 100 secondary datasets per primary dataset, totalling 10000 datasets. During the simulation of these secondary datasets we again take note of the trajectories that have been taken by all sister pairs. Fourth, from the prevalence of each trajectory in the secondary datasets we construct 95% confidence intervals for the trajectories of interest (Figure 3.2b, c, d), and it is evaluated if the prevalence of the trajectories in the primary dataset falls within the 95%CI of the respective secondary datasets.

**Table S3.5** recovery of trajectories taken according to the best models for each primary dataset. The procedure in which results are obtained are described above. Figure refers to the trajectories in Figure 3.2: (b) where do the pairs end up that have left state 1, (c) how did species pairs that are sympatric with differentiated elevational ranges end up there, and (d) how did species pairs become sympatric with overlapping elevations. Within refers to if the prevalence of each trajectory as simulated in the primary dataset falls within the 95%CI's of the secondary dataset. For primary prevalences that fall outside of the

95%CI the distance to the mean prevalence under the secondary simulations is expressed in standard deviations.

| Figure | Process | Within 95%CI | Under-estimated | Over-estimated | Dist. to mean | SDs to mean |
|---|---|---|---|---|---|---|
| 2b | ES | 75 | 15 | 10 | 0.16 | 3.3 |
| 2b | ED | 72 | 8 | 20 | 0.21 | 3.72 |
| 2b | EC | 83 | 17 | 0 | 0.18 | 4.55 |
| 2c | ES | 69 | 17 | 14 | 0.3 | 6.66 |
| 2c | ED | 69 | 14 | 17 | 0.3 | 6.66 |
| 2d | ES | 90 | 9 | 1 | 0.1 | 6.54 |
| 2d | ED | 63 | 5 | 32 | 0.28 | 3.54 |
| 2d | EC | 64 | 32 | 4 | 0.31 | 3.98 |

**Table S3.6** recovery of trajectories taken according to the model-averaged parameters for each primary dataset. See Table S3.5 for details.

| Figure | Process | Within 95%CI | Under-estimated | Over-estimated | Dist. to mean | SDs to mean |
|---|---|---|---|---|---|---|
| 2b | ES | 82 | 11 | 7 | 0.15 | 3.08 |
| 2b | ED | 76 | 7 | 17 | 0.19 | 3.31 |
| 2b | EC | 89 | 11 | 0 | 0.18 | 4.05 |
| 2c | ES | 70 | 15 | 15 | 0.26 | 4.44 |
| 2c | ED | 70 | 15 | 15 | 0.26 | 4.44 |
| 2d | ES | 96 | 3 | 1 | 0.15 | 6.56 |
| 2d | ED | 62 | 4 | 34 | 0.24 | 2.96 |
| 2d | EC | 60 | 37 | 3 | 0.26 | 3.09 |

### *Initial state analysis*

We made the assumption that species arise in allopatry with overlapping elevational ranges. However, species may already arise with differentiated elevational ranges. For instance, take the case where populations are situated on different mountain ranges reaching distinct peak altitudes. Differentiation in elevation may consequently appear to occur if populations consistently occupy the highest range of a mountain, but that these peak altitudes differ between geographic locations. This results in species arising in state 3 instead of state 1 (Figure 3.1). The frequency at which this might occur, and that this results in complete separation of elevational ranges between populations and new species, is uncertain, but cannot be ignored. We partially took this into account by varying the degree of elevational overlap at which we consider species to be elevational differentiated, but we performed an additional analysis where we estimated the frequency of state 3 speciation in our dataset.

We accounted for the possibility that species may arise in allopatry while differentiated in elevational range (state 3) by including an additional parameter, $\gamma$, which describes the probability that speciation occurs in state 1 relative to state 3. We added this parameter to two scenarios: (*i*) we fitted the complete model with all transitions and parameters (r12, r13, r15, r24, r25, r34, r45, and $\gamma$), and (*ii*) we fitted the model but instead have species transition from state 3 to state 1 (r12, r15, r24, r25, r31, r34, r45, and $\gamma$). Our motivation for this was that we could not be certain that species that are currently in state 1, we note that >62% of sister pairs and primarily the youngest pairs (Figure 3.3a) are in state 1, did not arise in state 3 and subsequently transitioned to state 1. We first fit each of the two scenarios to the empirical data using maximum likelihood (ML) and estimate the transition rates and $\gamma$, where $\gamma$ is constrained from 0-1. Second, we estimated a likelihood profile for both scenarios by incrementally varying $\gamma$ in steps of 0.01 from 0 to 0.3 in order to see which values of $\gamma$ fall within the 95%CI set, i.e. within 1.92 log-likelihood units of the ML estimate of $\gamma$. Preliminary analyses of larger step sizes showed that the likelihood profile did not have multiple peaks, supporting our analysis of the limited values for $\gamma$.

We found that for respectively (*i*) $\gamma$ = 3.55e-15 with 95%CI's from 0 to ~0.08, and (*ii*) $\gamma$ = 0.048 with 95%CI's from ~0.03 to ~0.11 (Figure S3.4). This overall suggests that the probability that species arise in a state of allopatry while elevationally differentiated is low for our particular dataset, but we cannot rule out that it does not occur at all.

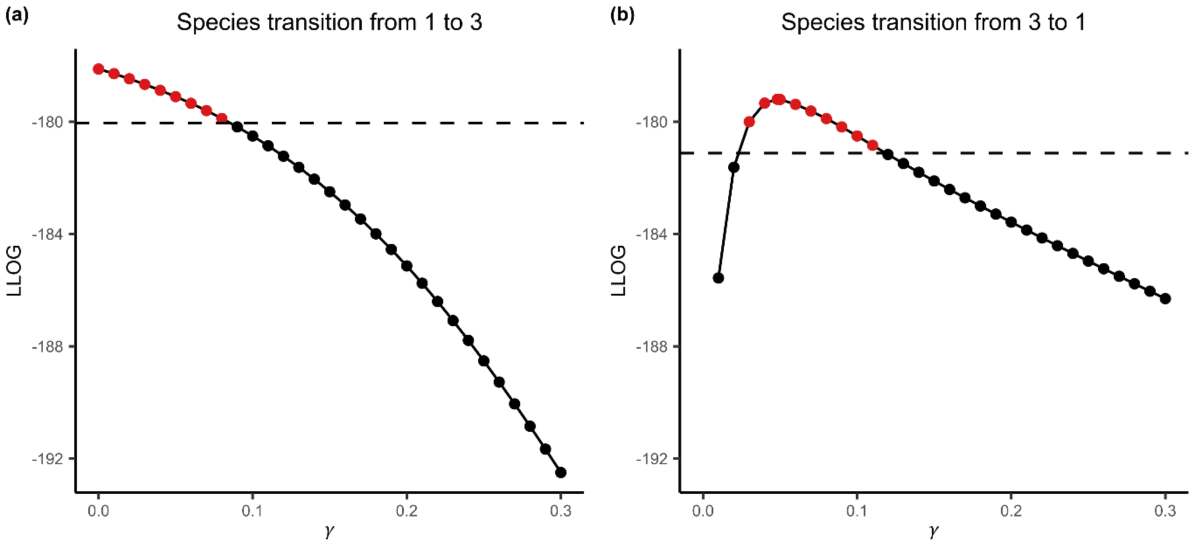

**Figure S3.4** Likelihood of elevational differentiation upon speciation (*γ*). (a) shows the likelihood profile for models where sister species can transition from allopatry without elevational differentiation to allopatry with elevational differentiation (state 1 → 3), and (b) shows the profile for models with the opposite transition (state 3 → 1) (Figure 3.1). The dashed lines represents the 95%CI respective to the maximum likelihood estimates. Frequencies of *γ* above the dashed line are highlighted in red and considered not significantly different.

## Appendix 3: Supplementary material Chapter 4

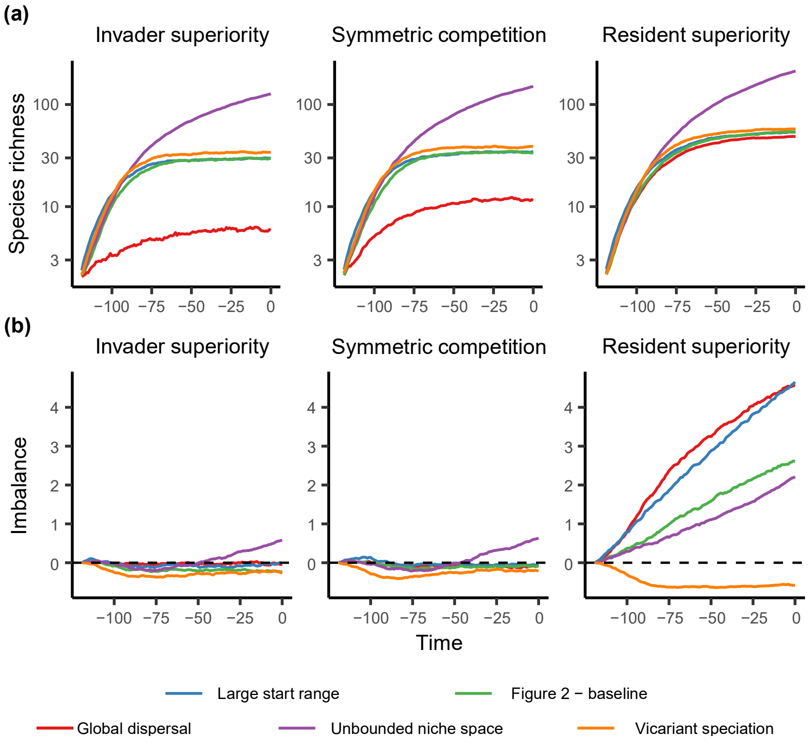

**Figure S4.1** The impact of model assumptions on a) trends in metacommunity species richness over time (mean across simulation runs) and b) phylogenetic imbalance at T = 120 (Sackin index, Appendix III). Colours indicate the five distinct versions of the model (see Appendix I for details) which were simulated under otherwise identical parameter values ($\psi$ = 0.25, $\lambda$ = 0.02, $\gamma$ = 0.25, $\sigma$ = 0.25, $\mu_{bg}$ = 0). The three columns represent the three modes of competition: Invader- superiority (left), symmetric competition (middle), and resident-superiority (right). Results shown are for 100 realisations per parameter combination.

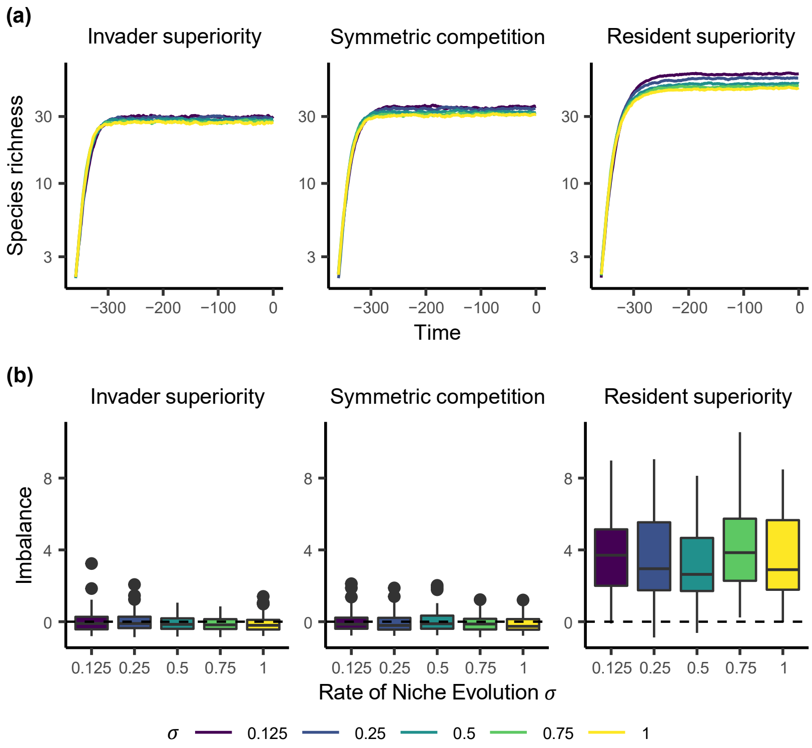

**Figure S4.2** The impact of the rate of niche evolution $\sigma$ on a) trends in metacommunity species richness over time (mean across simulation runs) and b) phylogenetic imbalance at T = 360 (Sackin index, Appendix III). The three columns represent the three modes of competition: Invader-superiority (left), symmetric competition (middle), and resident-superiority (right). Colours denote the rate of niche evolution $\sigma$, with lighter colours indicating faster rates of niche evolution. Results shown are for 100 simulation runs per parameter combination. Apart from $\sigma$, identical parameter settings were used ($\lambda$ = 0.02, $\gamma$ = 0.25, $\psi$ = 0.25, $\mu_{bg}$ = 0).

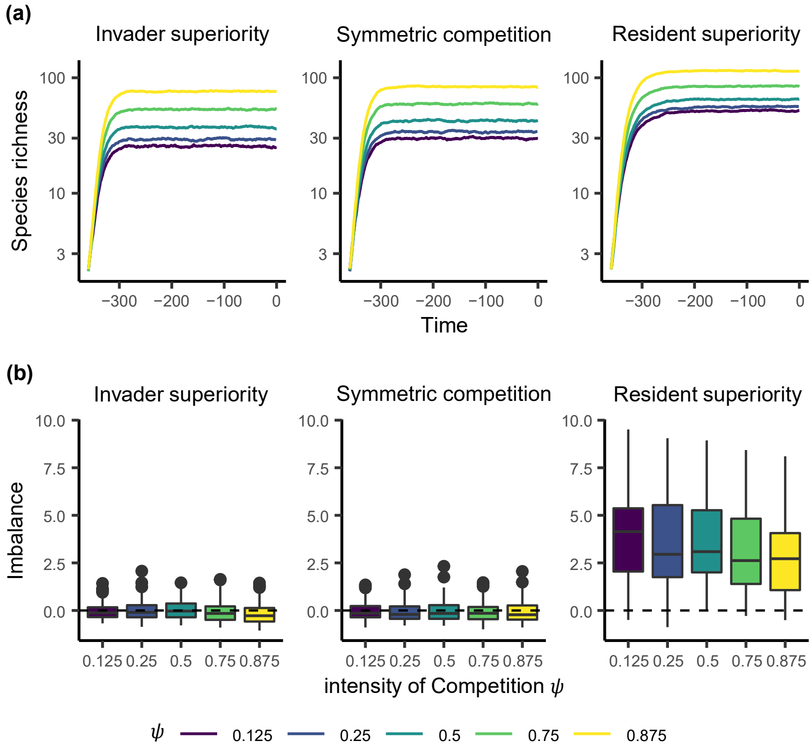

**Figure S4.3** The impact of competitive intensity $\psi$ on a) trends in metacommunity species richness over time (mean across simulation runs) and b) phylogenetic imbalance at T = 360 (Sackin index, Appendix III). The three columns represent the three modes of competition: Invader-superiority (left), symmetric competition (middle), and resident-superiority (right). Colours denote the intensity of competition $\psi$ where lighter colours indicate less intense competition. Results shown are for 100 simulation runs per parameter combination. Apart from $\psi$, identical parameter settings were used ($\lambda = 0.02$, $\gamma = 0.25$, $\sigma = 0.25$, $\mu_{bg} = 0$).

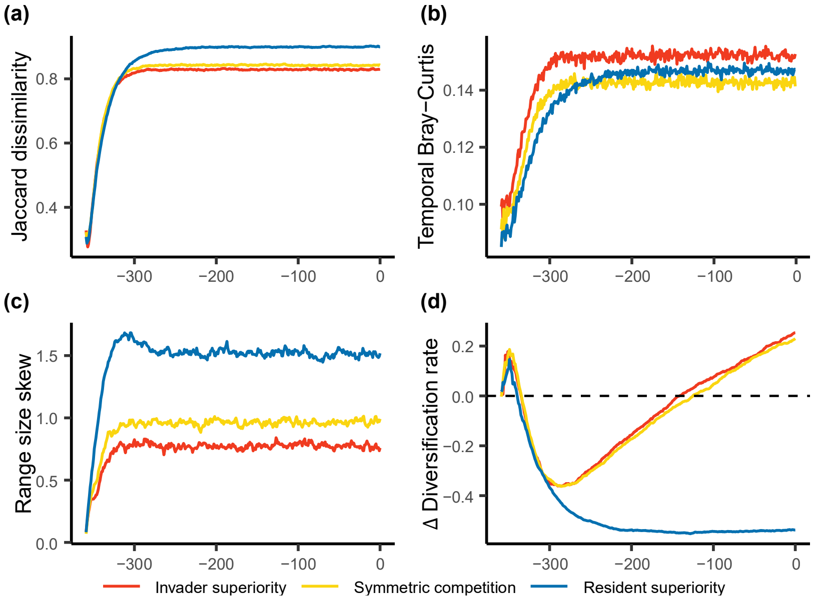

**Figure S4.4** The impact of arrival order on the outcome of competition for additional metrics. Colours denote the three modes of competition: Invader-superiority, symmetric competition, and resident-superiority. Plotted through time the metrics represent: a) Jaccard dissimilarity index calculated between adjacent sites; b) the temporal Bray-Curtis dissimilarity index, which indicates the average rate of change in community composition over time; c) the skew of the species range size distribution, where high values indicates few large and many small ranged species; d) Change in diversification rate Δr. Negative (positive) values of Δr indicate a slowdown (speedup) in diversification rate over time (Appendix III). Δr is calculated using the reconstructed phylogeny, explaining the increase in Δr over time for IS and SC as older lineages go extinct and information on past diversification is lost. Simulation parameters are identical to those shown in Fig. 2, with results showing the mean trend across 500 simulation runs. See Appendix III for further details on metrics.

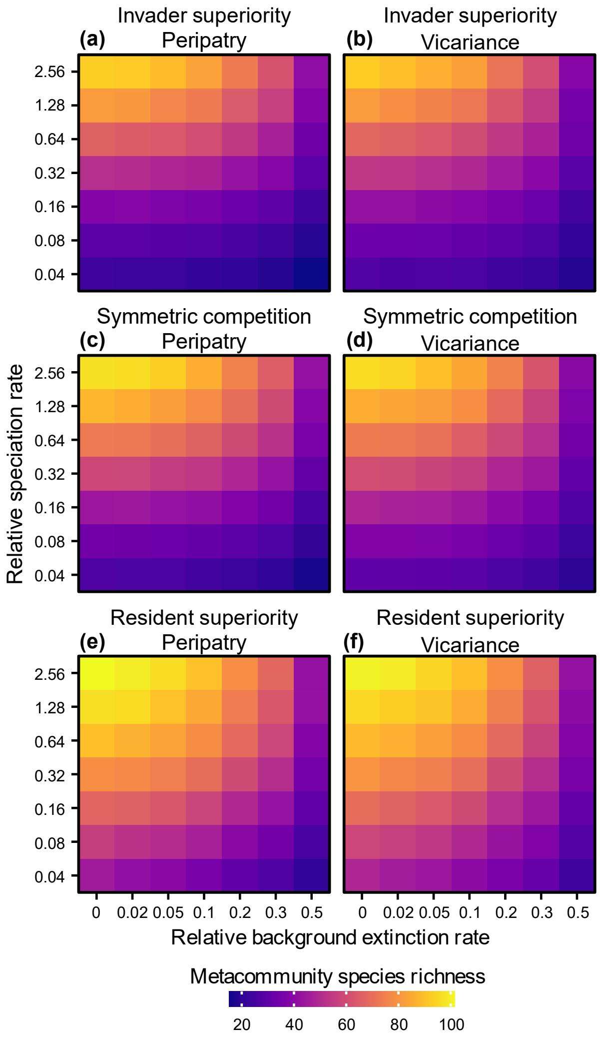

**Figure S4.5** The influence of the rate of population background extinction, speciation and speciation-mode on the absolute species richness expected under the IS, SC and RS model. a, c, e) peripatric speciation-mode and b, d, f) vicariance speciation-mode. On each plot, the y-axis and x-axis denote the speciation $\lambda$ and population background extinction $\mu_{bg}$ rates respectively, both calculated relative to the rate of colonisation, kept constant at $\gamma = 0.25$. Colours indicate the absolute number of species present in the metacommunity averaged across 100 simulation runs at $T = 360$. Competitive intensity ($\psi = 0.25$) and the rate of niche evolution ($\sigma = 0.25$) are kept constant for all simulations.

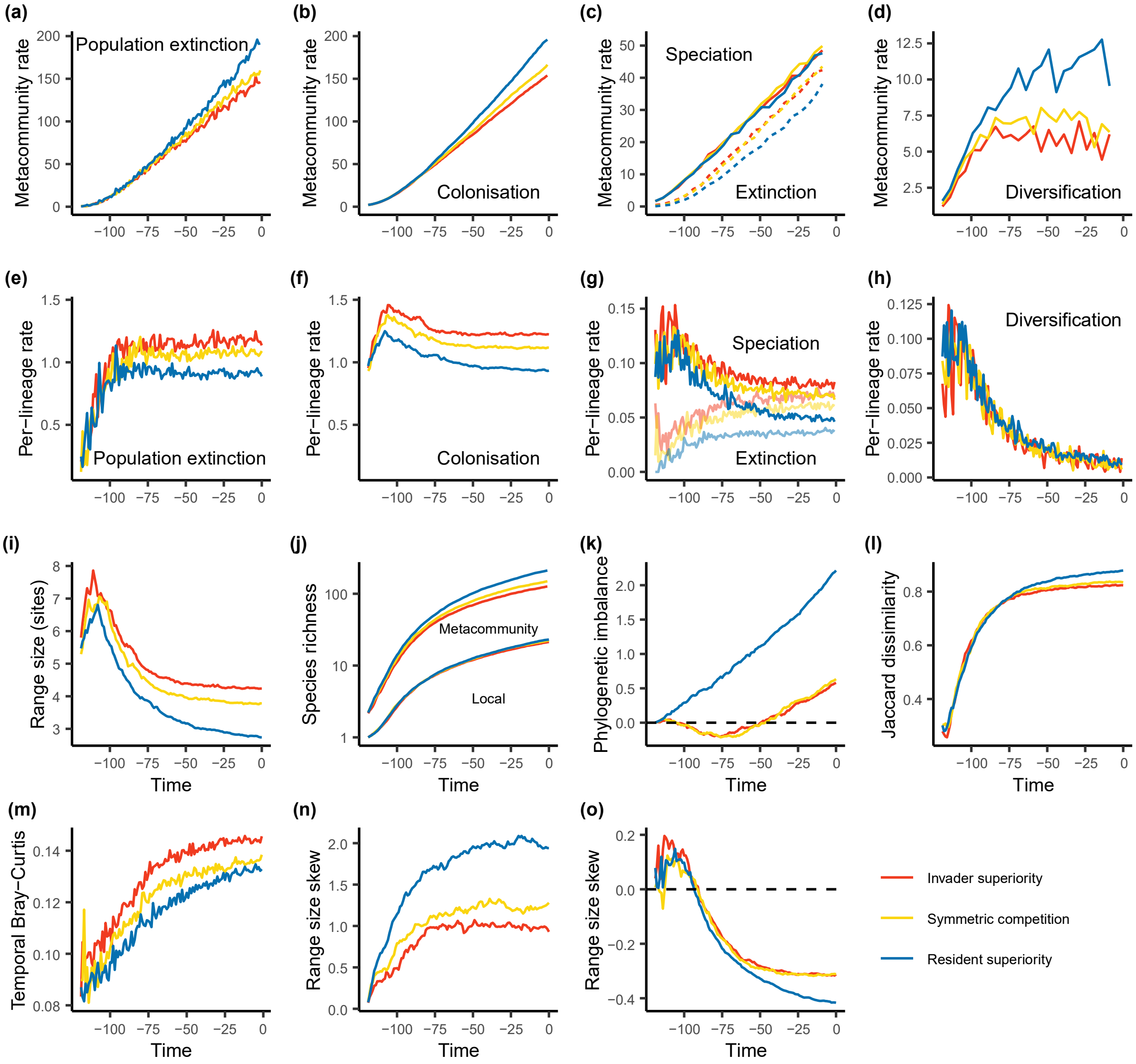

**Figure S4.6** The dependence of macroevolutionary dynamics on the presence or absence of priority effects when niche space is unbounded. Priority effects are represented by the RS model (blue) and is compared to the opposite scenario of IS (red) and an intermediate SC (yellow) model. Each plot shows the results for a different macroevolutionary rate or pattern, with the x-axis representing the time from the crown age to the present day. a-d) total metacommunity rate and e-h) mean per-lineage rate of a,e) population extinction; b,f) colonisation; c,g) cladogenetic speciation (bold) and species extinction (dashed/shaded); d,h) diversification; i) average range size; j) metacommunity and average local species richness; k) Sackin index of phylogenetic tree imbalance, where the dashed line represents the imbalance expected under a pure-birth model; l) Jaccard dissimilarity index calculated between adjacent sites; m) the temporal Bray-Curtis dissimilarity index, which indicates the average rate of change in community composition over time; n) the skew of the species range size distribution, where high values indicates few large and many small ranged species; o) change in diversification rate $\Delta r$ calculated on the reconstructed phylogeny. Values show the mean trend across 100 simulation runs under: $\psi = 0.25$, $\lambda = 0.02$, $\gamma = 0.25$, $\sigma = 0.25$, and $\mu_{bg} = 0$. See Appendix III for details on metrics used.

## Appendix 4.I – alternate modelling assumptions

Our baseline simulations assume a small starting range size, a peripatric model of speciation, a bounded niche space and nearest-neighbour dispersal. In addition to varying the rate of speciation ($\lambda$), background population extinction ($\mu_{bg}$), niche evolution ($\sigma$) and strength of competitive exclusion ($\psi$) in this baseline scenario, we also explored the impact on expected phylogenetic and spatial patterns of four alternate modelling assumptions: (i) a large starting range size of the ancestral species (ii) a vicariance model of speciation (iii) a model in which niche space is unbounded and (iv) a model where the assumption of nearest-neighbour dispersal is relaxed.

### Starting range size

In the resident-superiority model, local priority effects can lead to strong phylogenetic imbalance by enforcing asymmetries in range size, and thus rates of diversification, generated during peripatric speciation (Figs. 4.2 , 4.3 & 4.5). We show that when the speciation rate $\lambda$ is high relative to the rate of colonisation γ, expected phylogenetic imbalance is reduced (Fig. 4.4). This is because speciation leads to a reduction in range size (of 1 site in the peripatric model), reducing asymmetries in range size and rates of diversification among lineages. We therefore expected that for a given rate of speciation $\lambda$ and colonisation $\gamma$, a scenario in which the ancestral species fills the entire domain would lead to higher phylogenetic tree imbalance compared to when it just occupies a single site. We indeed find that a large starting range, results in higher phylogenetic imbalance when priority effects operate, with little effect on tree balance for the IS and SC models (Fig S4.1b). Thus, initial conditions can have an important effect on phylogenetic tree imbalance, with the impact of priority effects magnified when the ancestor is widespread. In contrast, while a large starting range size leads to species richness accumulating faster at the start of the radiation it does not alter the equilibrium species richness attained (Fig S4.1a).

### Vicariant speciation

Peripatric speciation results in asymmetry in the rate of speciation among lineages because range sizes between sister lineages are unequally split. In contrast, vicariant speciation is expected to result in a more equal split in range size and concomitantly more even speciation rates. To address how this alters the patterns expected under priority effects we implemented a vicariant speciation model. In this scenario, speciation is modelled as a per-species (rather than per-population rate), with the rate scaling linearly with range size (i.e. thus equal to the cumulative per-population speciation rate in the peripatric model). Second, when a species is selected to undergo speciation, we calculate the x-and y-dimension of the species' range. The dimension along which the species range will be split is then randomly chosen with a probability equal to the relative length of the range dimensions. In this way, species are more likely to be split perpendicular to their long axis (Pigot *et al.* 2010). Third, the species range is split at the mid-point of the selected dimension, resulting in two daughter lineages with, on average, equal range sizes. As our findings show, vicariance results in more balanced phylogenetic trees (Fig. 4.5d). This is the case under all competition scenarios, but is particularly strong when priority effects operate, leading to trees that are substantially more balanced than expected under a pure-birth model (Fig. S4.1b). Because fewer species have very small ranges under the vicariance model, rates of species extinction are reduced, especially in the invader-superiority and symmetric competition model. While the reduction in species extinction reduces the differences in equilibrium richness between the competition scenarios, priority effects still lead to higher species richness (Fig. S4.1a).

### Unbounded niche space

Whether there is a hard ecological limit to species richness continuous to be debated (Harmon & Harrison 2015; Rabosky & Hurlbert 2015). In our model we do not impose a carrying capacity directly, but an ecological limit to diversity is expected because of the finite number of sites and the limit to niche similarity of coexisting species. We tested how the impact of priority effects depend on the assumption that niche space is bounded, by exploring a scenario where there are no bounds to niche space (i.e. no repulsion away from the boundary) ($\alpha = 0$, $K = \infty$). As expected, when niche space is unbounded, species richness continues to increase over time, albeit at a declining rate (Fig. S4.1a). For a given clade age, priority effects lead to higher species richness than when priority effects are absent. Phylogenetic trees remain strongly unbalanced when priority effects are present, but not as unbalanced as when niche space is bounded (Fig. S4.1b). This can be explained because the species at the edge of niche space will experience more ecological opportunity and thus faster rates of diversification thus reducing the impact the priority effects. In contrast, the advantage of being at the edge of niche space also results in unbalanced phylogenetic trees under IS and SC models, which is not observed when niche space is bounded (Fig. S4.1b).

### Global dispersal

When dispersal only occurs between adjacent sites this may limit the rate of range expansion because many populations will not occur at the edge of the range or may be blocked from expanding by the presence of closely related and ecologically similar species. In contrast, with long distance dispersal events, species can form and then spread from multiple isolated fragments, increasing rates of spread. To test this effect of spatial structure we implemented a global dispersal model in which the population of a species can colonise any currently unoccupied site in the domain rather than just adjacent sites. As expected, we find that global dispersal facilitates even greater imbalance when priority effects are present, because species that arise early or evolve novel niches can more rapidly spread. In contrast, allowing global dispersal has little effect on phylogenetic tree shape under the IS and SC models (Fig S4.1b) but increases the relative difference in richness among competition scenarios (Fig S4.1a).

## Appendix 4.II – Simulating diversity dynamics

In order to simulate dynamics in continuous time we use the modified Gillespie algorithm for non-constant rates (Gillespie 1977; Allen & Dytham 2009). Specifically, (i) the waiting time ($\delta$) until the next colonisation $\gamma$, speciation $\lambda$ or population extinction $E$ event is drawn from an exponential distribution with a mean equal to the sum of these rates across all populations extant at time $t$. For speciation $\lambda$, these per-population rates are constant over time with the total rate dependent only on the number of extant populations $N$ at time $t$. For colonisation $\gamma$, per-population rates are constant but only populations at the edge of the species range (i.e. adjacent to an unoccupied neighbour in the four cardinal directions) are counted. In contrast, the per-population rate of extinction $E$ changes over time according to local species' niche overlap and the order of species arrival within sites. To calculate $\delta$ we therefore use the maximum possible rate of population extinction $E_{max}$ across all populations

$$E_{max} = \mu_{bg} + \mu_{comp}$$

which is the rate of population extinction assuming all species have identical niches (i.e. *OVL* = 1); (ii) at time $t + \delta$, mean niche values evolve by addition of random deviates from a normal distribution with mean = 0 and variance equal to $\sigma$ multiplied by $\delta$; (iii) at time $t + \delta$, the probability of any particular event occurring P is given by the ratio of the actual rates at time $t + \delta$ and the maximum rate,

$$P = \frac{\gamma + \lambda + E}{\gamma + \lambda + E_{max}}$$

If an event occurs (iv), then the type of event (colonisation, speciation, population extinction) is selected at random based on the actual rates of these processes at time $t + \delta$. Finally, (v) the population to undergo the event is sampled based on its actual rate. For speciation, all populations in the metacommunity are sampled with an equal probability. For colonisation, all edge populations are sampled with an equal probability. For population extinction, populations are sampled with relative probability *E*.

We note that in the symmetric competition model (SC) species potentially experience competition from both earlier and later arrivals (Fig. 4.1c). This would result in higher rates of competitive exclusion $\Omega$ and thus population extinction *E* in the SC compared to IS and RS models, confounding the effects of arrival order with the rate of population extinction. To avoid this, in practice we simulated the SC model in the same way as the RS model (i.e. disregarding niche overlap *OVL* from the nearest neighbouring species that arrive later than focal species *i*) but using a randomly permuted vector of species arrival times to determine which species is excluded. We note that while this procedure randomises the competitive superiority of species, it does not impact which species focal species i competes with as niche position is unaffected.

The SC model conforms to a scenario in which local coexistence depends on niche stabilising mechanisms (i.e. niche divergence) and we do not consider how niche equalising mechanisms (i.e. similar fitness (Chesson 2000)) could delay local competitive exclusion. However, because no species is at an intrinsic advantage, this effect of niche equalisation is present at the metacommunity scale, so that the number of sites occupied by equivalent competitors would undergo drift over time.

## Appendix 4.III – Assessing model output

Over the course of a simulation we record the (i) changes in local per-lineage colonisation and extinction rate; (ii) species' range position (and consequently community composition); and (iii) keep track of the timing of all species' extinction and speciation events and ancestor-descendent relationships.

Species' range position is used to quantify average species range size (i.e. the number of occupied sites per-species) and the skew of the range size frequency distribution (e.g. a positive skew would indicate few species with large ranges and many species with small ranges). Average local and metacommunity richness is calculated by quantifying the mean number of species within sites and the total number of unique extant species. Spatial turnover in community composition is calculated by quantifying the average Jaccard dissimilarity between adjacent sites. Note that differences in spatial turnover are related to the average species' range size, as smaller range size would mean higher turnover. Finally, we calculate the temporal turnover in meta-community composition at successive time points using the Bray-Curtis dissimilarity index (Baselga & Orme 2012; Baselga 2017). We account for ancestral persistence (i.e. the species with the largest range is seen as the ancestor under peripatric speciation) to avoid pseudo-turnover resulting from changes in species identity post-speciation. This metric illustrates meta-community turnover not only in species composition but also changes in relative occupancy (i.e. range size) through time.

Using the ancestor-descendent relationships of lineages we reconstruct the species phylogenetic tree. Using the paleoPhylo package (Ezard & Purvis 2009) we calculated the per-lineage speciation and species extinction rate per time bin at a 1 *T* intervals. In contrast to calculating turnover, speciation is treated as a cladogenetic process resulting in the birth of two daughter lineages. To reflect the information recorded in reconstructed molecular phylogenies, we also pruned extinct lineages from the tree and then quantified two metrics of tree shape. First, tree balance using the Sackin index (Mooers & Heard 1997; Blum & François 2005; Blum *et al.* 2006). The Sackin index is normalised according to a pure-birth model, with positive (negative) values indicating a greater (lower) imbalance compared to a pure-birth tree. Second, the relative change in reconstructed diversification rate using the *r*-statistic (Pigot *et al.* 2010; Etienne & Rosindell 2012),

$$\Delta r = \frac{ln\frac{L(T)}{L\left(\frac{1}{2}T\right)} - ln\frac{L\left(\frac{1}{2}T\right)}{L(0)}}{ln\frac{L(T)}{L\left(\frac{1}{2}T\right)} + ln\frac{L\left(\frac{1}{2}T\right)}{L(0)}}.$$

where *L(T)* is the number of lineages at time *T* and *L(0)* the initial number of lineages. We calculate *Δr* from the crown age, which means that *L(0)* = 2. Values of *Δr* below zero indicate that there has been a slowdown in diversification rate towards the present. The *r*-statistic is a more suitable metric for our purposes than the gamma statistic (Pybus & Harvey 2000; McPeek 2008) as it is independent of tree size.

## Appendix 4.IV – Invasion from outside the metacommunity

Our model corresponds to a closed metacommunity in which all species are descendants from the ancestral lineage present at the start of the simulation. For metacommunities smaller than the entire planet, however, species may also arrive from outside the metacommunity. As with declining diversification rates, priority effects are expected to result in a decline in invasion success over time as niche space is filled. However, given similar dynamics of diversification across competition modes, we hypothesised that niche filling would also result in a decrease in invasion success over time under the IS and SC models. We therefore performed an additional post hoc computational experiment in which we introduced a novel alien species to the metacommunity. Alien species were assigned an initial niche value ($x_{invasion}$) drawn at random from a uniform distribution with bounds $-K$ and $K$ ($K$ = 5) and were introduced to a single randomly selected site. For each simulation we introduced a single alien species at time point $T_{invasion}$, exploring eight different values of $T_{invasion}$ (5, 10, 15, 25, 50, 75, 100 and 125). We assume that intrinsic per-population rates governing the alien invader are equivalent to the native species, thus allowing the alien invader to colonise new sites, speciate, and go locally and globally extinct. We used the same parameter values as those presented in Fig. 2 ($\psi$ = 0.25, $\lambda$ = 0.02, $\gamma$ = 0.25, $\sigma$ = 0.25, and $\mu_{bg}$ = 0).

Rather than simulate metacommunities from scratch, and to reduce computational burden, we used the saved output from our previously performed simulations as starting points for our invasion experiment. Specifically, for a single simulation run, we extracted the state of the metacommunity at time point $T_{invasion}$, introduced the alien invader and then ran the simulation from that time-point. The simulation was stopped when the invader, or all of its evolutionary descendants, had gone extinct or when 195$T$ had expired since $T_{invasion}$, which ever condition was reached first. For each model of competition, we selected ten simulation runs and for each of these ran 100 repeat simulations for each of the eight invasion times resulting in are 1000 repeats per $T_{invasion}$ value. Here the repeats per $T_{invasion}$ within a simulation run capture the effects of random variation in selected site and niche position, whereas the repetition across simulation runs incorporates variability in the radiation of the metacommunity prior to invasion. For each invasion simulation we quantified the time until the invader, or all of its evolutionary descendants, had gone extinct.