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LETTER

Priority effects and the macroevolutionary dynamics of biodiversity

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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 and analyse 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 how 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 generation and maintenance of biodiversity.

KEYWORDS
adaptive radiation, community assembly, competition, extinction, invasion, metacommunity, niche filling, niche incumbency, priority effects, speciation

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 (De Meester et al., 2016; Fukami, 2015). 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 (Odion et al., 2010; Westoby et al., 1989)—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; Fukami, 2015; Urban & De Meester, 2009; 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 (Gillespie et al., 2020; Stroud & Losos, 2016). 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 (Alroy, 1996; Rosenzweig & McCord, 1991). 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 (Price, 2008; Rabosky, 2013; Weir, 2006). 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 (Pigot et al., 2018; Weir & Price, 2011).

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 (Economo & Sarnat, 2012; Pepke et al., 2019; Ricklefs & Bermingham, 1999; Wilson, 1959). 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 experiments on a computer simulated 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 (Odion et al., 2010; Westoby et al., 1989), or because invaders are subject to Allee effects (Henriques-Silva et al., 2019). Invaders may have a transient competitive advantage if they have escaped from their natural enemies (enemy release hypothesis (Colautti et al., 2004; Keane & Crawley, 2002)) or carry novel weapons (e.g. pathogens; Diez et al., 2010; Lymbery et al., 2014; Sheppard & Schurr, 2019; Vilcinskas, 2015). 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 (γ), speciation (λ), population extinction (E) and niche evolution (σ). The simulation starts with a single lineage occupying a randomly selected site within a square lattice (5×5 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 (Figure S1, Appendix I). We refer to each occupied site in a species' geographic range as a population. Colonisation occurs at per-population rate γ, 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 (Figure S1, Appendix I).

Speciation occurs at per-population rate λ 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 'vicarance scenario', simulated by splitting the species' range into two approximately equal size areas (Figure 4, Appendix I).

Species' niches, representing the ecological requirements of a species (e.g. seed sizes consumed by a granivorous bird), are modelled as Gaussian distributions, each 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 σ. 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; Gavin 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 (Figures S1 and S6, Appendix I).

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

A population suffers extinction at per-population rate E_i with the extinction of a species occurring when its last population is extirpated. E_i is a summation of the rate of population background extinction μ_{bg} which is constant across populations and over time, and also the rate of population competitive exclusion Ω_i,

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

where Ω_i depends on a constant μ_{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 β was set *a priori* ($\beta = 30$) so that Ω 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 ψ (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 (Clarke et al., 2017; Inman & Bradley, 1989). 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 (Figure 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 (Figure 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 (Figure 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 (Figure 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 (Figure 1c; Appendix II).

Exploration of parameter space and summary statistics

We simulated the model in continuous time using the modified Gillespie algorithm (Allen & Dytham, 2009; Gillespie, 1977) (Appendix II). For each of the three models of competition, we examine varying rates of (a) speciation ($\lambda = 0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64$), (b) population background extinction ($\mu_{bg} = 0, 0.005, 0.0125, 0.025, 0.05, 0.075, 0.125$), (c) rate of niche evolution ($\sigma = 0.125, 0.25, 0.50, 0.75, 1.00$, Figure S2), and (d) the level of niche overlap at which the rate of population competitive exclusion Ω is half μ_{comp} ($\psi = 0.125, 0.25, 0.5, 0.75, 0.875$, Figure S3). We keep species niche breadth ($s = 0.15$), colonisation rate ($\gamma = 0.25$) and the constant controlling the rate of competition exclusion ($\mu_{comp} = 5$)
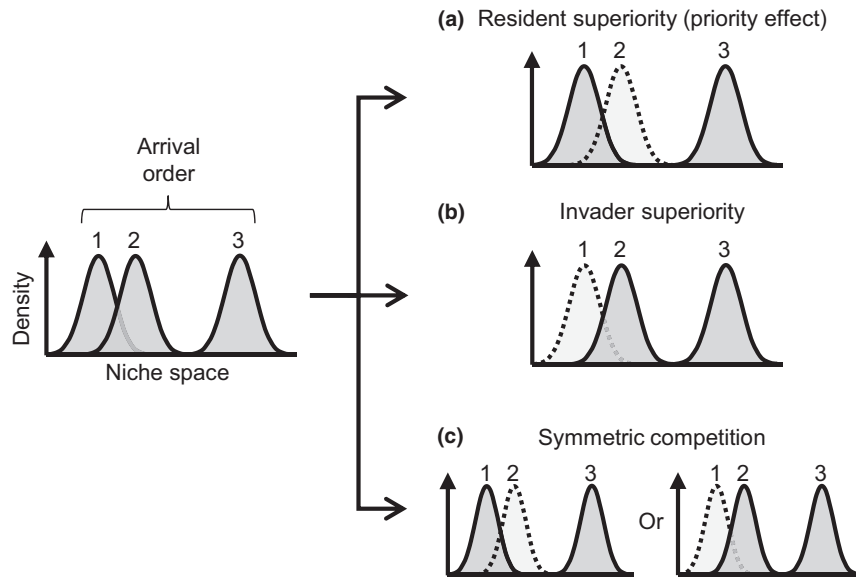
FIGURE 1 Impact of arrival order on the outcome of competition. An exemplar community is represented consisting of three species with niches distributed across an arbitrary axis and competition occurring between nearest neighbours. The order of arrival presented here is arbitrary (i.e. unrelated to niche 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.

fixed, as their effects are expected to be partially redundant with other parameters. For instance, increasing the colonisation rate γ will have a similar effect to reducing the rates of speciation λ, population background extinction μ_{bg} and niche evolution σ, while increasing niche breadth s would have a similar effect to reducing ψ or increasing μ_{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 (a) all species have gone

extinct, or (b) 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 (Figure 2, Figures S1–S3). Early in the radiation, richness accumulates rapidly (Figure 2j) because most sites contain few if any species, rates of population extinction are lower than rates of colonisation (Figure 2a and b), and species average range size thus expands (Figure 2i). This leads to low rates of species extinction and an
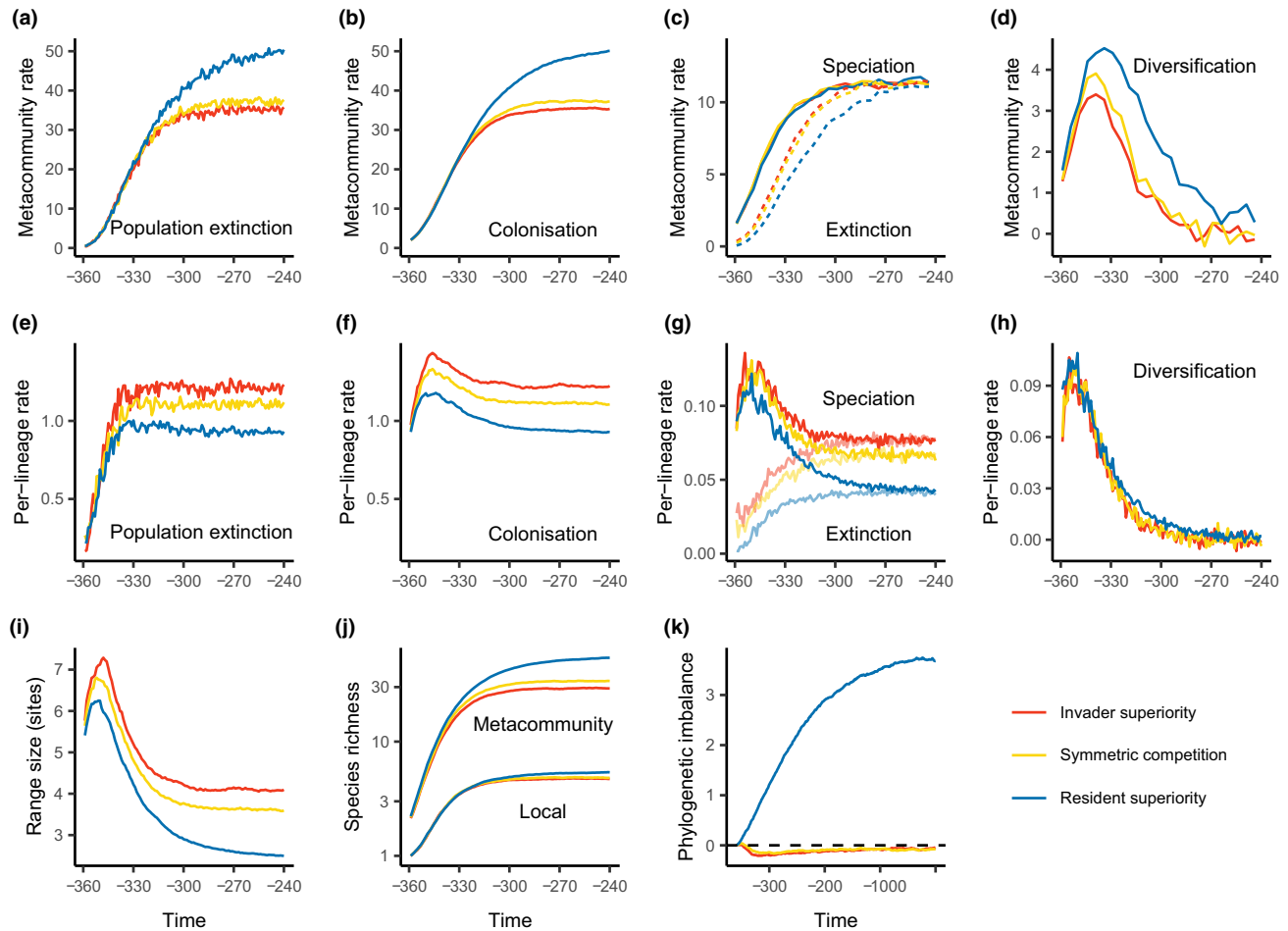
FIGURE 2 Dependence of macroevolutionary dynamics on the presence or absence of priority effects. Priority effects are represented by the RS model (blue) and is compared to the opposite scenario of IS (red) and an intermediate SC (yellow) model, where the probability of competitive exclusion is independent 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 $\mu_{bg} = 0$. See Appendix III for details on metrics used.

accelerating rate of speciation at both the metacommunity and lineage level (Figure 2c and g). As local richness accumulates, there is an increase in the rate of population extinction (Figure 2e), eventually converging on the rate of colonisation (Figure 2f), so that average range size peaks and subsequently declines (Figure 2i). The decline in average range size causes an increase in per-lineage rate of species extinction, decrease in speciation (Figure 2g), and a decline in the metacommunity and per-lineage rate of diversification (Figure 2d and h). While a diversification slowdown is also evident in the reconstructed phylogeny, this pattern is eroded over time under the IS and SC models as high rates of species extinction prune the oldest lineages from the tree (Figure S4d). Eventually local sites, and then the metacommunity, reach a dynamic equilibrium in which species richness fluctuates stochastically around a steady state (Figure 2j).

Metacommunity and local species richness

Although the temporal accumulation of species richness is qualitatively similar across competition scenarios, local and metacommunity richness varies (Figure 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 (Figures S1–S3). 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 (Figures 2c,g and 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
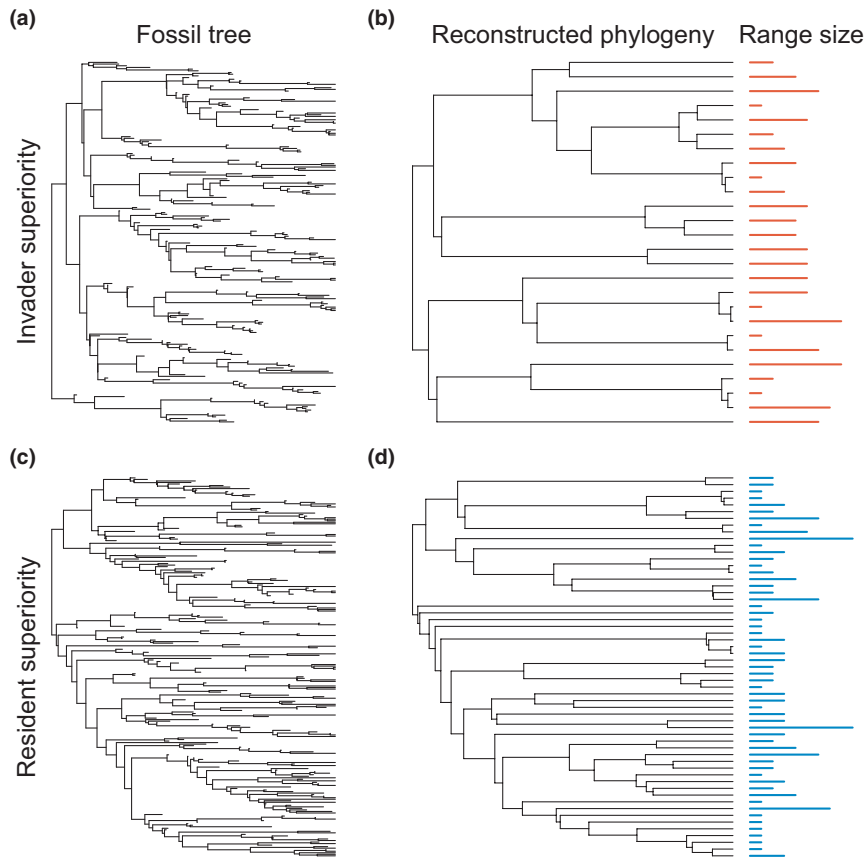
FIGURE 3 Impacts of priority effects on diversification dynamics. Phylogenetic trees from a single exemplar simulation are shown for respectively the IS (a and b) and RS (c and d) model. In (a and c) fossil trees are shown including extinct lineages, while (b and d) show the reconstructed phylogeny (i.e. including only extant lineages). Coloured bars at the tips of the phylogeny in (b and 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 $\mu_{bg} = 0$.
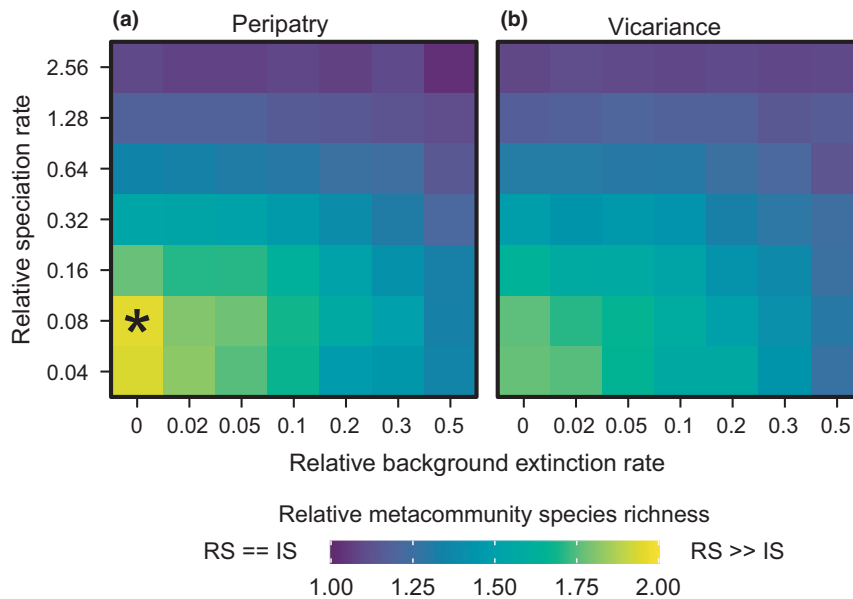

FIGURE 4 Influence of the rate of population background extinction, speciation and speciation-mode on the relative metacommunity species richness expected under the IS and RS model. (a) peripatric and (b) vicariance speciation-mode. On each plot, the y-axis and x-axis denote the speciation λ and population background extinction μ_{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.
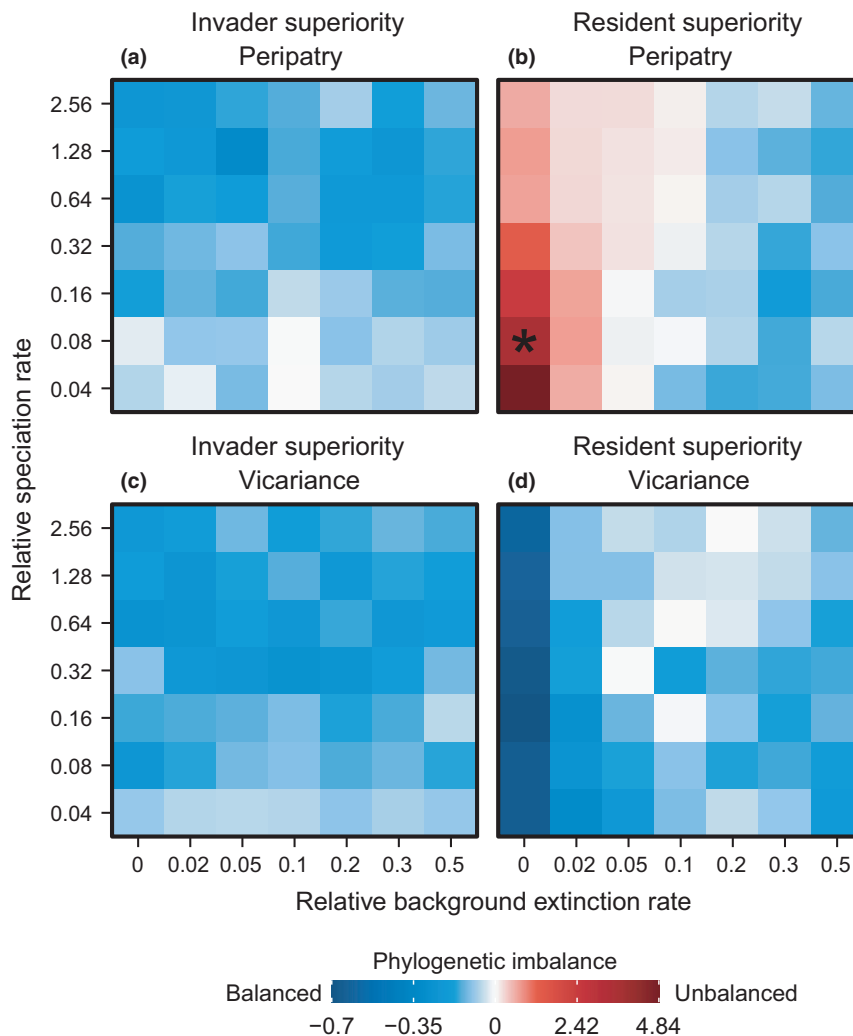
FIGURE 5 Influence of the rate of population background extinction, speciation and speciation-mode on phylogenetic tree imbalance expected under the (a and c) IS and (b and d) RS model and under (a and b) peripatric and (c and d) vicariant speciation-modes. On each plot, the y-axis and x-axis denote the rate of speciation λ and population background extinction μ_{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 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.

the metacommunity (Figure 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 (Figure 2a and b), but lower per-lineage rates of population extinction, colonisation and speciation (Figure 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 (Figure 2c).

The higher metacommunity richness under the RS model is evident across a broad region of parameter space (Figures S1–S3), but varies according to key model parameters (Figure 4). With high rates of population background extinction μ_{bg}, the strength of priority

effects is reduced leading to more similar metacommunity richness across competition scenarios (Figure 4). In contrast, when the rate of speciation λ is low relative to the rate of colonisation γ 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 (Figure 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 (Figure 4, Figure S1 and S5).

Phylogenetic tree imbalance

Priority effects have a major impact on phylogenetic imbalance (Figure 3). In the IS and SC models, phylogenies are more balanced than expected under a pure-birth model (Figure 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 (Figure 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 (Figure 5b and d).

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 (Figures 2k, 3 and 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 (Figure 5d). The impact of priority effects on phylogenetic tree shape vary depending on rates of population background extinction μ_{bg} and speciation λ. When population background extinction is rapid μ_{bg} the impacts of priority effects are eroded, leading to trees that converge on similar levels of balance to the IS and SC models (Figure 5a and b). Equally, when speciation λ is rapid relative to colonisation γ, 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 (Moen & Morlon, 2014; Rabosky, 2009). 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 (Figures S1 and S6).

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 (Betancur-R et al., 2012; Brockhurst et al., 2007; Fukami et al., 2007; Gillespie, 2004; 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 IV). We found that across all competition scenarios, the survival time of the invading alien lineage is lower when introduced later in the radiation (Figure 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 the invader-superiority model, 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.

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 (Blum & François, 2006; Mooers & Heard, 1997). 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 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 (Figure 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 (Figure 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 (Fukami & Morin, 2003; Morton & Law, 1997; Steiner & Leibold, 2004), particularly when there
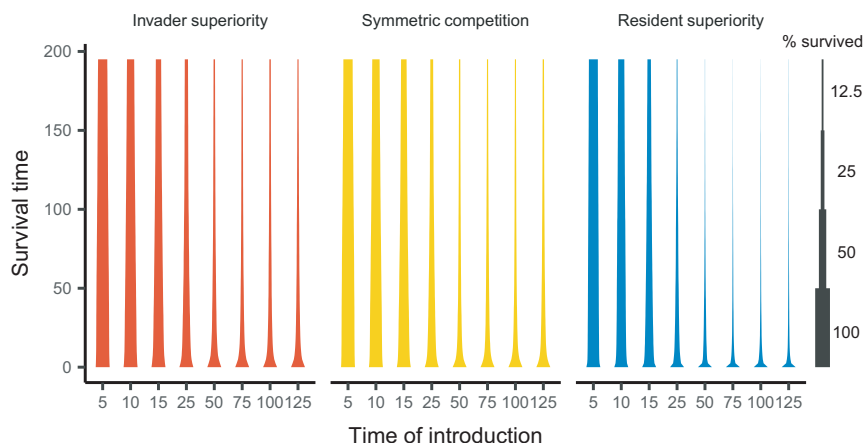

FIGURE 6 Success of invaders from outside the metacommunity in the presence and absence of priority effects. Colours represent the three modes of competition: IS (red), SC (yellow), and RS (blue). The x-axis indicates the time from the start of the simulation when an invader from outside the metacommunity 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 IV for further details.

is a diverse species pool, because of greater variability across sites in the order of species arrival (Chase, 2010; Fukami, 2015; Steiner, 2014). 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 (Figure 2, Figure S4), 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.

AUTHOR CONTRIBUTIONS
BRR, DJM and ALP conceived the study. BRR developed the analytic approach, performed analyses and wrote the initial manuscript. All authors provided comments throughout and helped to substantially improve the manuscript.

DATA AVAILABILITY STATEMENT
All simulated data (https://doi.org/10.5522/04/14400947) and code (https://doi.org/10.5522/04/14397920) required to perform the simulations is deposited in a publicly available repository.

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REFERENCES

Aguilée, R., Gascuel, F., Lambert, A. & Ferriere, R. (2018) Clade diversification dynamics and the biotic and abiotic controls of speciation and extinction rates. *Nature Communications*, 9(1).

Allen, G.E. & Dytham, C. (2009) An efficient method for stochastic simulation of biological populations in continuous time. *BioSystems*, 98, 37–42.

Alroy, J. (1996) Constant extinction, constrained diversification, and uncoordinated stasis in North American Mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127, 285–311.

Betancur-R., R., Ortí, G., Stein, A.M., Marceniuk, A.P. & Alexander Pyron, R. (2012) Apparent signal of competition limiting diversification after ecological transitions from marine to freshwater habitats. *Ecology Letters*, 15, 822–830.

Blum, M.G.B. & François, O. (2005) On statistical tests of phylogenetic tree imbalance: The Sackin and other indices revisited. *Mathematical Biosciences*, 195, 141–153.

Blum, M.G.B. & François, O. (2006) Which random processes describe the tree of life? A large-scale study of phylogenetic tree imbalance. *Systematic Biology*, 55, 685–691.

Brockhurst, M.A., Colegrave, N., Hodgson, D.J. & Buckling, A. (2007) Niche occupation limits adaptive radiation in experimental microcosms. *PLoS One*, 2, 1–4.

Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, 5, 49.

Chase, J.M. (2003) Community assembly: When should history matter? *Oecologia*, 136, 489–498.

Chase, J.M. (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science*, 328, 1388–1391.

Clarke, M., Thomas, G.H. & Freckleton, R.P. (2017) Trait evolution in adaptive radiations: Modeling and Measuring interspecific competition on phylogenies. *American Naturalist*, 189, 121–137.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, 7, 721–733.

Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sunderland, MA: Sinauer Associates Inc.

De Meester, L., Vanoverbeke, J., Kilsdonk, L.J. & Urban, M.C. (2016) Evolving perspectives on monopolization and priority effects. *Trends in Ecology & Evolution*, 31, 136–146.

Diez, J.M., Dickie, I., Edwards, G., Hulme, P.E., Sullivan, J.J. & Duncan, R.P. (2010) Negative soil feedbacks accumulate over time for non-native plant species. *Ecology Letters*, 13, 803–809.

Duncan, R.P., Cassey, P., Pigot, A.L. & Blackburn, T.M. (2019) A general model for alien species richness. *Biological Invasions*, 21, 2665–2677.

Economo, E.P. & Sarnat, E.M. (2012) Revisiting the ants of melanesia and the taxon cycle: Historical and human-mediated invasions of a tropical archipelago. *American Naturalist*, 180, 1–16.

Ezard, T.H.G. & Purvis, A. (2009) paleoPhylo: Free software to draw paleobiological phylogenies. *Paleobiology*, 35, 460–464.

Fukami, T. (2015) Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology Evolution and Systematics*, 46, 1–23.

Fukami, T., Beaumont, H.J.E., Zhang, X.X. & Rainey, P.B. (2007) Immigration history controls diversification in experimental adaptive radiation. *Nature*, 446, 436–439.

Fukami, T. & Morin, P.J. (2003) Productivity-biodiversity relationships depend on the history of community assembly. *Nature*, 424, 423–426.

Gillespie, D.T. (1977) Exact stochastic simulation of coupled chemical reactions. *Journal of Physical Chemistry*, 81, 2340–2361.

Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, 303, 356–359.

Gillespie, R.G., Bennett, G.M., De Meester, L., Feder, J.L., Fleischer, R.C., Harmon, L.J. et al. (2020) Comparing adaptive radiations across space, time, and taxa. *Journal of Heredity*, 111, 1–20.

Hawkes, C.V. (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *American Naturalist*, 170, 832–843.

Henriques-Silva, R., Kubisch, A. & Peres-Neto, P.R. (2019) Latitudinal-diversity gradients can be shaped by biotic processes: New insights from an eco-evolutionary model. *Ecography*, 42, 259–271.

Hubbell, S.P. (2001) *The unified theory of Biodiversity and Biogeography*. Monographs in Population Biology. Princeton, NJ: Princeton University Press.

Hull, P. (2015) Life in the aftermath of mass extinctions. *Current Biology*, 25, R941–R952.

Inman, H.F. & Bradley, E.L. (1989) The overlapping coefficient as a measure of agreement between probability distributions and point estimation of the overlap of two normal densities. *Communications in Statistics - Theory and Methods*, 18, 3851–3874.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17, 164–170.

Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, 175, 316–334.

Lymbery, A.J., Morine, M., Kanani, H.G., Beatty, S.J. & Morgan, D.L. (2014) Co-invaders: The effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife*, 3, 171–177.

MacArthur, R.H. (1972) *Geographical ecology. Patterns in the distribution of species*. New York, NY: Harper and Row.

McInnes, L., Baker, W.J., Barraclough, T.G., Dasmahapatra, K.K., Goswami, A., Harmon, L.J. et al. (2011) Integrating ecology into macroevolutionary research. *Biology Letters*, 7, 644–646.

Moen, D. & Morlon, H. (2014) Why does diversification slow down? *Trends in Ecology & Evolution*, 29, 190–197.

Mooers, A.O. & Heard, S.B. (1997) Inferring evolutionary process from phylogenetic tree shape. *The Quarterly Review of Biology*, 72(1), 31–54.

Morton, R.D. & Law, R. (1997) Regional species pools and the assembly of local ecological communities. *Journal of Theoretical Biology*, 187, 321–331.

Nicolau, J. (2002) Stationary processes that look like random walks – The bounded random walk process in discrete and continuous time. *Economic Theory*, 18, 99–118.

Nuismer, S.L. & Harmon, L.J. (2015) Predicting rates of interspecific interaction from phylogenetic trees. *Ecology Letters*, 18, 17–27.

Odion, D.C., Moritz, M.A. & Dellasala, D.A. (2010) Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology*, 98, 96–105.

Pepke, M.L., Irestedt, M., Fjeldså, J., Rahbek, C. & Jønsson, K.A. (2019) Reconciling supertramps, great speciators and relict species with the taxon cycle stages of a large island radiation (Aves: Campephagidae). *Journal of Biogeography*, 46, 1214–1225.

Pigot, A.L. & Etienne, R.S. (2015) A new dynamic null model for phylogenetic community structure. *Ecology Letters*, 18, 153–163.

Pigot, A.L., Jetz, W., Sheard, C. & Tobias, J.A. (2018) The macroecological dynamics of species coexistence in birds. *Nature Ecology & Evolution*, 2, 1112–1119.

Pigot, A.L., Phillimore, A.B., Owens, I.P.F. & Orme, C.D.L. (2010) The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. *Systematic Biology*, 59, 660–673.

Price, T. (2008) *Speciation in birds*. Greenwood village, CO: Roberts and Co.

Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P. et al. (2014) Niche filling slows the diversification of Himalayan songbirds. *Nature*, 509, 222–225.

Rabosky, D.L. (2009) Ecological limits and diversification rate: Alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, 12, 735–743.

Rabosky, D.L. (2013) Diversity-dependence, ecological speciation, and the role of competition in macroevolution. *Annual Review of Ecology Evolution and Systematics*, 44, 481–502.

Ricklefs, R.E. & Bermingham, E. (1999) Taxon cycles in the Lesser Antillean avifauna. *Ostrich*, 70, 49–59.

Rosenzweig, M.L. & McCord, R.D. (1991) Incumbent replacement: Evidence for long-term evolutionary progress. *Paleobiology*, 17, 202–213.

Sheppard, C.S. & Schurr, F.M. (2019) Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia. *Global Ecology and Biogeography*, 28, 222–237.

Simpson, G.G. (1953) *The major features of evolution*. New York, NY: Columbia University Press.

Steiner, C.F. (2014) Stochastic sequential dispersal and nutrient enrichment drive beta diversity in space and time. *Ecology*, 95, 2603–2612.

Steiner, C.F. & Leibold, M.A. (2004) Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. *Ecology*, 85, 107–113.

Stroud, J.T., Giery, S.T., Outerbridge, M. & Feeley, K.J. (2019) Ecological character displacement alters the outcome of priority effects during community assembly. *Ecology*, 100, 1–10.

Stroud, J.T. & Losos, J.B. (2016) Ecological opportunity and adaptive radiation. *Annual Review of Ecology Evolution and Systematics*, 47, 507–532.

Svoboda, P., Lindström, E.S., Ahmed Osman, O. & Langenheder, S. (2018) Dispersal timing determines the importance of priority effects in bacterial communities. *ISME Journal*, 12, 644–646.

Tanentzap, A.J., Brandt, A.J., Smissen, R.D., Heenan, P.B., Fukami, T. & Lee, W.G. (2015) When do plant radiations influence community assembly? The importance of historical contingency in the race for niche space. *New Phytologist*, 207, 468–479.

Urban, M.C. & De Meester, L. (2009) Community monopolization: Local adaptation enhances priority effects in an evolving metacommunity. *Proceedings of the Royal Society B-Biological Sciences*, 276, 4129–4138.

Valentine, J.W., Jablonski, D., Krug, A.Z. & Roy, K. (2008) Incumbency, diversity, and latitudinal gradients. *Paleobiology*, 34, 169–178.

Vilcinskas, A. (2015) Pathogens as biological weapons of invasive species. *PLoS Path*, 11, 1–5.

Weir, J.T. (2006) Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, 60, 842.

Weir, J.T. & Price, T.D. (2011) Limits to speciation inferred from times to secondary sympatry and ages of hybridizing species along a latitudinal gradient. *The American Naturalist*, 177, 462–469.

Westoby, M., Walker, B. & Noy-meir, I. (1989) Opportunistic management for rangelands not at equilibrium. *Journal of Range Management*, 42, 266–274.

White, A.E., Dey, K.K., Stephens, M. & Price, T.D. (2021) Dispersal syndromes drive the formation of biogeographical regions, illustrated by the case of Wallace's Line. *Global Ecology and Biogeography*, 1–12.

Wilson, E.O. (1959) Adaptive shift and dispersal in a tropical ant fauna. *Evolution*, 13, 122.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.