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RESEARCH ARTICLE

Increased dispersal explains increasing local diversity with global biodiversity declines

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Abstract

The narrative of biodiversity decline in response to human impacts is overly simplistic because different aspects of biodiversity show different trajectories at different spatial scales. It is also debated whether human-caused biodiversity changes lead to subsequent, accelerating change (cascades) in ecological communities, or alternatively build increasingly robust community networks with decreasing extinction rates and reduced invasibility. Mechanistic approaches are needed that simultaneously reconcile different aspects of biodiversity change, and explore the robustness of communities to further change. We develop a trophically structured, mainland-archipelago metacommunity model of community assembly. Varying the parameters across model simulations shows that local alpha diversity (the number of species per island) and regional gamma diversity (the total number of species in the archipelago) depend on both the rate of extirpation per island and on the rate of dispersal between islands within the archipelago. In particular, local diversity increases with increased dispersal and heterogeneity between islands, but regional diversity declines because the islands become biotically similar and local one-island and few-island species are excluded (homogenisation, or reduced beta diversity). This mirrors changes observed empirically: real islands have gained species (increased local and island-scale community diversity) with increased human-assisted transfers of species, but global diversity has declined with the loss of endemic species. However, biological invasions may be self-limiting. High-dispersal, high local-diversity model communities become resistant to subsequent invasions, generating robust species-community networks unless dispersal is extremely high. A mixed-up world is likely to lose many species, but the resulting ecological communities may nonetheless be relatively robust.

KEYWORDS
Anthropocene, biodiversity, community assembly, community dynamics, dispersal, ecology, invasion, simulation

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1 | INTRODUCTION

Multiple human-associated pressures are driving changes to biological diversity worldwide, leading to both academic and popular concern over the impending 'biodiversity crisis' and possible 'Sixth Mass Extinction' (Kolbert, 2014; Wilson, 2016). In particular, there is great concern that the number of species per unit area (alpha diversity) is declining due to land use changes and intensification (Newbold et al., 2015), that species-level rates of endangerment and extinction are increasing thus reducing the total number of species (gamma diversity; Ceballos et al., 2015; Pimm et al., 2014), and that land use change combined with the transport of species between different geographic locations is resulting in biological homogenisation (reduced beta diversity), as well as causing the extinction of localised species whose ranges have been invaded (Blackburn et al., 2004; Magurran et al., 2015; Olden et al., 2018). Taken together, these works strongly support the contention that 'biodiversity' is threatened, however it is measured.

In contrast, other studies suggest that alpha, beta and gamma diversity trajectories depend on the spatial scale and locations studied (McGill et al., 2015). Many studies have found that local alpha diversity is increasing in some locations while declining in others, with average alpha remaining similar, or possibly even increasing slightly (Dornelas et al., 2014; Thomas & Palmer, 2015; Vellend et al., 2013). At a larger scale, regional diversity has mainly increased despite reduced global (gamma) diversity: the number of plant species on oceanic islands has increased with plant invasions despite the extinctions of many island-endemic species (Sax & Gaines, 2008), the number of plant species per country or state is increasing despite regional losses (Vellend et al., 2017), and the number of mammal species has increased in most European countries over the last 8000 years despite many species having become extinct globally (Hatfield et al., 2022). And, in contrast to studies reporting homogenisation at some scales (above), land use changes may have increased beta diversity at many spatial scales for most of the last millennium because different species are associated with different 'natural' and human-modified ecosystem types (Martins et al., 2022). This flurry of studies generating different directions and strengths of alpha, beta and gamma diversity change in different spatial, temporal and geographical contexts has led to confusion and disputes in the literature, undermining the development of consensus measures to manage biodiversity (e.g. Leung et al., 2020; Leung et al., 2022; Leung et al., 2022a, 2022b, 2022c; Loreau et al., 2022; Mehrabi & Naidoo, 2022; Murali et al., 2022; Puurtinen et al., 2022).

Further confusion relates to the extent to which these derived ecosystems and ecological communities become more or less resistant to further biological change through time. Invasion biology identifies the potential for community 'cascades' and 'collapse' in which community turnover, both losses and invasions of species, begets further turnover (Kehoe et al., 2021; Polis et al., 2000). This perspective holds that the initial changes to community food webs lead to successive changes, resulting in further losses and increased potential for subsequent invasions as community networks reorganise. Adaptive community dynamics (Carroll et al., 2023; Vellend, 2016), in contrast, holds that changes to the identities and relative abundances of species in a given location should generally increase the robustness of certain community properties as they adjust to both the (new) biological and physical environments, potentially increasing their resistance to further invasion. Thus, the dynamic processes of community reorganisation as well as the outcomes, especially scales of diversity change, are debated.

Community ecology has already seen that altered rates of movement (inter-patch mixing) drive local diversity and homogenisation simultaneously (Gilbert et al., 1998; Mouquet & Loreau, 2003), as in Figure 1. We further develop the theory of inter-patch mixing, henceforth dispersal, and how dispersal affects not only the observed patterns of biodiversity across scales but also ongoing and future changes to communities by considering temporal turnover and invasibility. Using a mainland-archipelago model, we find that changing the rate of dispersal of organisms between heterogeneous islands within the archipelago is qualitatively sufficient to generate the variety of contrasting biodiversity trends observed in nature; while immigration events and local extirpations do generate ongoing community dynamics, high dispersal generally produces communities that are robust to further invasion. Simple dynamics in the model can generate multiple patterns in the simulated communities in space and time, helping to resolve several apparent paradoxes in assessments of different aspects of biodiversity change.

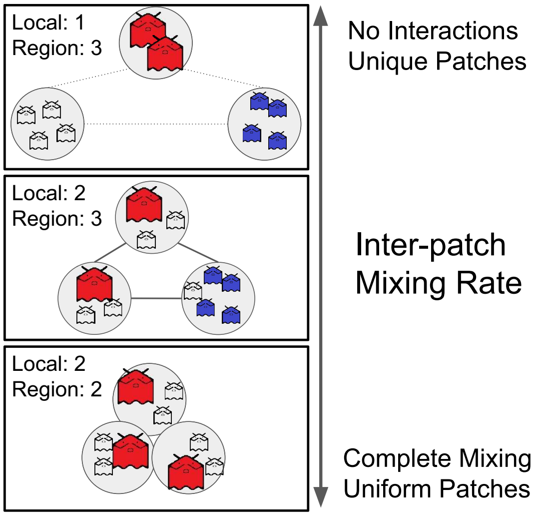

FIGURE 1 Hypothesised relationships of local and regional diversity with dispersal. In communities with negligible dispersal (top), local communities (alpha) support few species (here, one critter species per patch/island), but different species (high beta), creating high regional gamma diversity (here, three critter species in total). High dispersal (bottom) generates richer local communities (here, two per patch) but the communities are the same as one another due to species mixing, and hence total regional diversity is only two species. At intermediate mixing (middle panel), various outcomes are possible, here showing local communities as diverse as complete mixing, and regional richness as diverse as no mixing (one variant of the intermediate dispersal hypothesis).

2 | MATERIALS AND METHODS

To investigate the relationship between dispersal, heterogeneity, measures of biodiversity across scales, and robustness to change, we develop a model of community assembly. We begin by placing the model we develop in an ecological context. We then describe the construction of our model mathematically, beginning with the (singular) pool and average interaction matrix. We discuss how we combine multiple patches, dispersal and the inclusion of stochastic events. We finally describe the numerical evaluation of our model, before finishing with a discussion of how we varied parameters and analysed results.

Pseudocode for the core processes is provided in the supplemental information for transparency and replication (Janssen et al., 2020), and the full simulation code is available (see Data Availability Statement, Fagan (2023)).

2.1 | Model description

Community ecology is no stranger to contradictory or counter-intuitive results and a mismatch between data and theory, including May's seminal result that complex communities are unlikely to be stable (May, 1972), a view not necessarily held by empirical ecologists (Allesina & Tang, 2015). The ensuing debates have required ecologists and mathematicians to understand which mechanisms and assumptions need to be changed in order for models to usefully reflect reality, leading to valuable developments in theory (Allesina & Tang, 2015) and in the interpretation of empirical data (Chase, 2003; Coyte et al., 2021; Pennekamp et al., 2018). Both theoretical and empirical studies consistently point to the importance of size- and trophic structure in shaping local communities, and to the role of community assembly in forming functional ecosystems, where by community assembly we mean the sequential local rearrangement of communities based on arrivals—long distance dispersal—and extinctions (Chase, 2003; Coyte et al., 2021; Fukami, 2015; Law & Morton, 1996; Massol et al., 2017; Morton & Law, 1997). The importance of both the structure of communities and space, which affect dispersal and interactions, have been emphasised in recent studies (Coyte et al., 2021; Galiana et al., 2018; Qian & Akçay, 2020; Serván & Allesina, 2021). Increased dispersal can potentially lead to complex biodiversity trends. Examples include increased alpha by enlarging the effective immigrant pool, but reduced beta via homogenisation of communities or the maximisation of local diversity at intermediate dispersal (Mouquet & Loreau, 2003), but still more complex patterns may emerge (Haegeman & Loreau, 2014; Kneitel & Miller, 2003). Our simulations that incorporate both dispersal and local community dynamics generate peak local diversities at intermediate dispersal when environments differ between patches with the peak height increasing with the heterogeneity between patches, and contrasting patterns in alpha, beta and gamma diversity.

Our model is an extension of community assembly, which mirrors island biogeography, and our analyses include inter-patch mixing. In a community assembly method, one seeks stable and complex systems by constructing a regional pool (a metaphorical mainland) from which species can migrate to initially empty patches (islands) via small initial populations. This method is known to successfully create systems of moderate size that can be resistant to further invasion from the pool in a theoretically robust and consistent manner (Law & Morton, 1996; Morton & Law, 1997). Thus, we have two major components to the model: community interactions and movement. We summarise the model in Figure 2 and briefly touch on its features here; we describe them further in the following sections and Supplemental Information.

The community interactions are created by following the process of Law and Morton (Law & Morton, 1996). First, the numbers of basal and consumer species in the species pool are decided, and then each species is randomly assigned a body size. Body sizes are then used to determine species properties, trophically structured interactions and interaction strengths. These are then considered fixed for the duration of an assembly simulation. While size-structured in that basal species function as autotrophs and consumers as heterotrophs that exploit autotrophs and other heterotrophs within a size range smaller than themselves, in principle similar outcomes are expected for any kind of consumer–consumed interaction network. Community interactions are normally assumed to take place in between arrivals—time scale separation—but we allow them to proceed continuously in parallel to facilitate the study of dispersal. We also then allow interaction strengths to vary between patches to reflect how environmental conditions may influence interspecific interactions.

In the model, we differentiate species movement between long-range pool–patch immigration and short-range patch–patch dispersal. The simulations begin with the species pool (conceptual mainland with fixed species properties and populations) and no species present within a focal network of similar but not identical patches (the conceptual archipelago, see our section entitled Multiple patches). Species immigrate to the archipelago (drawn at random from the pool, a neutral process) by sending a sub-population into a single patch (conceptual island; dashed arrows in Figure 2, sub-populations do not deplete pool population). The rate of immigration can be varied, although we focus here on one rate of immigration which is similar to the rate of community interactions but consider sensitivity to this variable in the Supplemental Information. If immigrants of a new species establish a population, it results in colonisation. Hence it is possible to evaluate the robustness of communities to subsequent colonisation as the fraction of possible immigration events resulting in colonisation; conceptually the invasibility of communities. At the end of a simulation, we test the capacity of each community (considering each patch separately) to resist invasion by deliberately and separately introducing each species not already present from the species pool.

As communities establish in each patch, individuals from those communities are neutrally mixed with individuals ('dispersal') from other communities (see our section entitled Dispersal between patches, vertical arrows in Figure 2), varying from zero mixing to complete mixing. The patches—in our case 10—are arranged in a ring, so

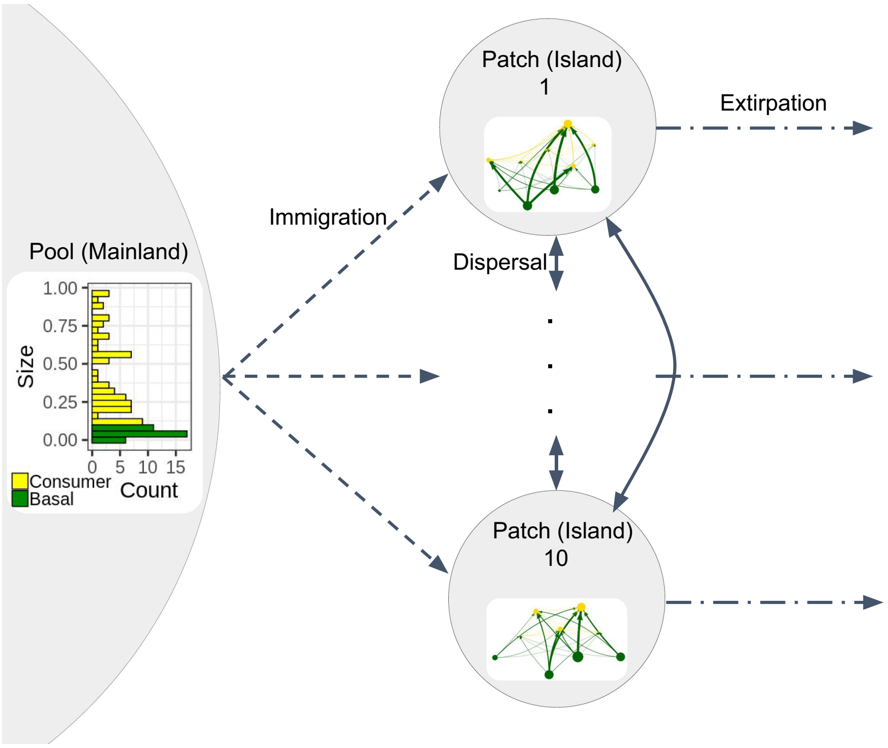

FIGURE 2 Model set-up at multiple scales. Our model begins with a fixed size-structured pool of species (left) with size-structured predation relations (histogram of size (vertical axis), with green for basal species and yellow for consumer species) and a fixed number of patches. The patches are allowed to differ abiotically from each other, slightly changing the strengths of interspecific interactions. Throughout the simulation, immigration can occur in which a sub-population of a species is drawn randomly from the pool and 'tries' to colonise a randomly selected patch (dashed lines). The sub-population successfully establishes if its per-capita growth rate is positive for the given patch without dispersal. Species that successfully establish are then subject to community dynamics within their patch food webs (with the size of each circle corresponding to a species' biomass and thickness of connecting lines representing the amount of flow), and can disperse in proportion to their abundance (along the double-headed arrows) to neighbouring patches (here patches are connected as a ring). Dot-dash lines from each patch indicate both deterministic extirpations (arising from community interactions) and also random, neutral extirpation events. The histogram here represents the pool used for the simulations in Figure 3, and the patch networks are representatives from a single time step of the no dispersal simulation. Network visualisation uses foodwebviz (Pawluczuk & Iskrzynski, 2022).

communities are up to five dispersal steps away from one another. Thus, our island archipelagos operate as metacommunities. When discussing variation in dispersal, we focus here on this between-patch mixing rate. We refer to pool-to-patch movement of species as 'immigration' and patch-to-patch movement as 'dispersal' (Figure 2).

Species extirpations, that is, losses from a single patch, and extinctions, that is, losses from the entire archipelago with re-invasion possible from the pool, take place (dash-dotted arrows in Figure 2). These are commonly driven by community dynamics, but we also include a stochastic element, applied at the patch level as is commonly adopted in stochastic metapopulation and metacommunity models to mimic local disasters including potentially human-mediated ones (see Supplemental Information for the no stochastic extirpation case). Thus, we include both deterministic (via community network dynamics) and stochastic components of species removals from communities.

Our simulation results allow us to explore the interactions between an ecologically justified model, dispersal, heterogeneous environments and the pool–patch structure. These simple modifications to community assembly are sufficient to recreate the observed phenomenon of per island alpha diversity increases and archipelago-scale gamma diversity declines. They are also sufficient to allow us to explore the impacts of our parameter choices on beta diversity measured as the spatial Jaccard dissimilarity index between patches at an instant in time, the temporal turnover measured as the Jaccard dissimilarity index through time within a patch and the final invasibility of the system (see Sections 2.7.1 and 2.7.2), which characterise whether our communities stabilise through time within islands and across the entire archipelago.

2.2 | Pool and interaction matrix construction

A mainland (species pool)–island (patch, local community) framework was selected to consider the impacts of different (inter-patch) dispersal rates on the balance between local community diversity (patch-level α) and regional (all patches γ) scales, and the compositional differences between communities (β). This approach was both computationally tractable and relevant to the real world, where numbers of species per oceanic island have often grown with increased human-assisted dispersal (increased α), while the extinction of endemic species (reducing global γ) associated with biological invasions (new community interactions and structures) is greatest in such locations (Duncan et al., 2013; Sax & Gaines, 2008). The methodology for constructing a species pool and the notation (including the numbering on parameters k_1 through k_6) used follow previous literature by Law and Morton (1996), whose approach was informed by Cohen et al. (1993).

A pool of 100 species, 34 basal and 66 consumer, is constructed by first assigning each species a number q_i drawn from uniform distributions on $(-2, -1)$ if basal and $(-1, 0)$ if a consumer unless otherwise specified. The size of species i is then $s_i = 10^{q_i}$ [henceforth labelled grams, but in principle representing a general measure of size (Law & Morton, 1996)]. Basal species have positive intrinsic growth rates and negative intraspecific interactions, but do not interact with other basal species. As a result, basal species abundance decreases primarily as a result of consumer consumption. Consumer species eat anything smaller than themselves [but have a built-in size preference as in real-world food webs (Cohen et al., 1993)], have negative intrinsic growth rates (that result in death if they run out of prey), and have no intraspecific interactions. Both basal and consumer species can be eliminated via too much consumption by their own consumers.

In what follows, we provide an explicit mathematical description of how the average growth rate ($\bar{r}_i$ for species i) and interaction terms ($\bar{a}_{i,j}$ for species i and j) are calculated. We then explain how these terms can be modified between patches to allow patch-level environmental heterogeneity to be captured.

2.2.1 | Intrinsic rate of increase

To construct species i's intrinsic growth (or loss) rate r_i (units per day), the mean is set to

$$\bar{r}_i = \begin{cases} 10^{-1-0.25q_i} & \text{for } i \text{ basal} \\ -0.1 & \text{for } i \text{ consumer.} \end{cases}$$

The basal intrinsic growth rate is empirically motivated (Blueweiss et al., 1978; Fenchel, 1974): a linear relationship is fitted to $\log r$ as a function of log body weight (see appendix of Law & Morton, 1996). Consumers rely on consuming prey to balance their intrinsic loss rate in order to survive/avoid starvation.

2.2.2 | Species intra-actions and basal biomass

To construct basal species i's intraspecific interactions ($a_{i,i}$), we set the mean to

$$\bar{a}_{i,i} = -r_i s_i / k_5$$

where $k_5 = 100$ (grams times species abundance density) determines the basal equilibrium biomass. This is so that each basal species has the same maximum carrying capacity when measured in terms of biomass with no consumers and we thus constrain the maximum basal biomass that a patch supports to 3400 g per volume (patch). As noted above, consumer species i has $a_{i,i} = 0$ (i.e. no intra-specific competition or density-dependent growth).

2.2.3 | Species interactions

To construct average species interactions $\bar{a}_{i,j}$, $i \neq j$, we compare the relative sizes and types of the species. We take the constants $k_1 = 0.01$ (units per time and species abundance density) to be the scale of the interaction strength relative to the growth rates, take $k_2 = 10$ to be the preferred size ratio of predator to prey, take $k_3 = 0.5$ to be the willingness to deviate from the preferred prey size and take $k_4 = 0.2$ to be the energy efficiency from consuming prey (Law & Morton, 1996).

Then the mean effect of species j on species i is

$$\bar{a}_{i,j} = \begin{cases} 0 \quad \text{if larger of } i,j \text{ is basal} \\ -k_1 \exp\left(-\left(\log_{10}\left(\frac{k_2 s_i}{s_j}\right)/k_3\right)^2\right) \\ \text{if } s_i < s_j \text{ and } j \text{ consumer} \\ -\bar{a}_{j,i} k_4 s_j / s_i \quad \text{if } s_j < s_i \text{ and } i \text{ consumer.} \end{cases}$$

Here, a basal species does not interact with species smaller than itself. If the larger species j is a consumer, then the inner expression of $-\left(\log_{10}\left(\frac{k_2 s_i}{s_j}\right)/k_3\right)^2$ provides diminishing returns as the prey deviates from the consumer's preferred size: k_2 determines the location of the maximum and k_3 the penalty for deviation. The size ratio and efficiency k_4 are then used to convert the abundance density from prey species to consumer species. Note that the gain to a consumer from consuming the prey and the loss to the prey from being consumed are not independent and are of opposite sign.

2.2.4 | Lotka–Volterra model

The average interactions $\bar{a}_{i,j}$ then can be used as a 100×100 Lotka–Volterra interaction matrix. In this case, the model in the absence of dispersal and environmental heterogeneity is

$$\dot{x}_i = x_i\left(r_i + \sum_{j=1}^{100} \bar{a}_{i,j} x_j\right)$$

for species $1 \leq i \leq 100$ with the abundance density of species i written as x_i and its time derivative as $\dot{x}_i$. The term $\left(r_i + \sum_{j=1}^{100} \bar{a}_{i,j} x_j\right)$ is the per capita growth rate of species i, which can be used to determine if species i could grow from a small population. Finally, we note that this system of equations captures all community- or patch-scale ecological dynamics with linear responses.

2.3 | Parallel community assembly

We now highlight our additions to and points of departure from the Law and Morton model of the previous section.

2.3.1 | Multiple patches

Instead of considering only a single community assembly process, we now construct multiple communities which model small environmental differences between discrete patches. We set a number of patches, here 10, fix the species pool, and then used the mean interactions $\bar{a}_{i,j}$ exactly as defined above, to generate patch specific interactions ${}_p a_{i,j}$ (unless there is no environmental heterogeneity).

For a patch *p*, each element of the associated interaction matrix is given by a random sample from a normal distribution truncated at 0 to preserve the sign of the element. That is

$$\begin{gathered} {}_p a_{i,j} = \operatorname{sgn}\left(\bar{a}_{i,j}\right) {}_p v_{i,j} \\ {}_p v_{i,j} \sim \text{TruncatedNormal}_{(0,\infty)}\left(\mu = |\bar{a}_{i,j}|, \sigma = k_6 |\bar{a}_{i,j}|\right) \end{gathered}$$

where sgn is the sign function, $\text{TruncatedNormal}_{(0,\infty)}$ is the truncated normal distribution (i.e. the distribution conditional on the event that a draw is from the range $(0, \infty)$ (Chopin, 2011), implemented in the `rtnorm` `R` package (Dzemski, 2018)), $|\cdot|$ takes the absolute value, and $k_6 = 0.1$ is the coefficient of variation of the underlying normal distribution. Since $k_6 = 0.1$, we expect all interaction matrices to be broadly similar, but to differ in exact magnitude (but not the sign of the interaction). Our highly heterogeneous environments case doubles k_6 to 0.2, while the homogeneous case takes ${}_p a_{i,j} = \bar{a}_{i,j}$. (All draws from the truncated normal distributions are independent.)

As all patches in a given run of the simulation share the same pool, we need not vary the pool in the same way. We still allow for variation in the parameters of the basal and consumer species by sampling the intrinsic growth/loss rates analogously with a fixed coefficient of variation:

$$\begin{gathered} r_i = \operatorname{sgn}\left(\bar{r}_i\right) \rho_i \\ \rho_i \sim \text{TruncatedNormal}_{(0,\infty)}\left(\mu = |\bar{r}_i|, \sigma = 0.1 |\bar{r}_i|\right). \end{gathered}$$

2.3.2 | Dispersal between patches

We also allow movement between patches following a network that is, in principle, arbitrary but in practice set to a one-dimensional torus (a ring). For each pair of patches we set a (positive) resistance to dispersal defined between them (taken, but not required, to be symmetric). If the resistance is infinite, no dispersal can occur directly between those two patches. We take the lower bound in our simulations to be a resistance of 1, at which 'full dispersal' takes place. Each species is then assigned a 'speed' (taken to be 1 for all species here), and together these define a dispersal (rate) matrix *D* which describes how quickly species abundance densities move between patches. We take the diagonal of *D* to be the negative of the (non-diagonal elements of the) column sums to conserve mass. Note that *D* is banded, corresponding to preventing abundance from changing species when dispersing from one patch to another. Hence, for species *i* on patch *p*, the rate of change of its abundance density is

$${}_p\dot{x}_i = {}_p x_i \left(r_i + \sum_{j=1}^{100} {}_p a_{i,j\,p} x_j \right) + \sum_{p'} {}_{p,p'} D_{ip'} x_i$$

where the additional labels capture the patch and the additional term captures movement of species *i* to and from patch *p*.

2.3.3 | Events and time scales

The Law and Morton model results in final, static, uninvasible communities (or cycles of communities) using time scale separation and by alternating between community dynamics and migration dynamics. We instead simultaneously assemble multiple interconnected communities to examine how they change through time. In addition to (neutral, local) immigration events, we first add their complement: extirpation (neutral, local extinction) events. This replicates local stochastic disasters. The implementation is similar for both. For immigration events, a species *i* is selected uniformly at random from the pool and a destination patch *p* is selected uniformly at random from the patches. If the per capita growth rate (see Lotka–Volterra model, above) is positive a small initial population (abundance of 0.4) is added to that patch (see Section S5.A.1). For extirpation events, if the species *i* is present on patch *p*, it is instead removed by setting its local abundance density ${}_p x_i$ to 0.

To numerically resolve the differences in time scale between immigration and extirpation events and community dynamics, we assign to each event an exponential waiting time. The exponential distribution's rate is the magnitude of the largest eigenvalue of the interaction matrices multiplied by a multiplier (taken to be 0.1, 1 or 10 independently as a simulation parameter for each of immigration and extirpation, as seen in Figure S11). The largest eigenvalue of the interaction matrices can be interpreted as the natural rate at which the interactions as a whole take place. Hence, the events should take place on a similar time scale as the fluctuations induced by community dynamics. We then numerically resolve our simulations using R's deSolve package (Hindmarsh, 1983; R Core Team, 2021; Soetaert et al., 2010), which implements the lsoda algorithm (Petzold, 1983) and can handle discrete events with continuous dynamics. This is as an alternative to permanence methods, which require time scale separation (see Hofbauer & Sigmund, 1988, 1998; Law & Morton, 1996).

2.4 | Meta-analysis

Our results in Figure 4 include only some of the parameter variations simulated. Here, we detail how the various runs differ from each other. Parameters and their combinations are given explicitly in Tables S1–S3. We also note our usage of R's tidyverse package for data handling and plotting (Wickham et al., 2019), the `patchwork` package for plotting (Pedersen, 2020) and the foreach package for parallelisation (Microsoft & Weston, 2020).

2.4.1 | Number and configuration of simulations

For a given parameter set, 10 different pools, each with 10 different patches, are generated. For simplicity, patches are configured in a ring (i.e. … ↔ 10 ↔ 1 ↔ 2 ↔ …) whose links are each assigned a single dispersal value; see the construction of D above. Each pool is then assigned 10 independent histories, which define 10 different simulation runs, allowing for the possibility of exploring pool-related emergent structure. Each run then contains 10 α values through time, 1 γ value through time, 45 spatial β values through time, 10 temporal β values through time (we fix the time difference to 1 / 100th the simulation length for computational efficiency) and 10 patch-level end of simulation invasibility calculations. These are all derived from the presence and absence of species in the 10 communities in the system.

2.4.2 | Variation of parameters

We vary the following parameters: the basal size lower bound, the consumer size upper bound, the coefficient of variation when sampling the interaction matrices, the (multiplier on the) rate of immigration events, the (multiplier on the) rate of extirpation events up to the exclusion of such events and the rate of dispersal (see Table S2). All other parameters in the system are fixed (see Table S1). We provide a full table of the parameters and how we vary them in combination in the Supplemental Information (Table S3). We vary these parameters as a robustness check on our parameter choices and conclusions. As discussed elsewhere in the main text, we provide alternative plots in the Supplemental Information. We finish with ~ 27,900 simulations completed. The remainder (~ 7500) failed due to memory or computing time constraints as discussed in the Supplemental Information.

To combine the results into Figure 4; Figures S10 and S11, for each simulation we take the median values of α, spatial β and temporal β (among all patches and over all times between 1×10^4 and 6.5×10^4 time units) and median values of γ (over all times) and end of simulation invasibility (see below). Figure 4 is then composed of these values for simulations with immigration and extirpation rate multipliers of 1 and no changes to the pool parameters (see Pool and Interaction Matrix Construction), with values aggregated by dispersal and interaction matrix coefficient of variation and presented using standard notched box-and-whisker plots (Wickham, 2016) and means (shown as lines and crosses). This prevents simulation length from biasing the analysis.

2.4.3 | Jaccard index

In order to quantify how patches differ from each other within a time step (spatial dissimilarity, spatial β) or how patches differ from themselves across time (temporal turnover, temporal β), we use the Jaccard (dissimilarity) index on the corresponding presence–absence data from our simulations as implemented in the `vegan` `R` package (Jaccard, 1912; Oksanen et al., 2022). Specifically, if A is the set of species present in one patch and B is the set of species present in a different patch at the same time (spatial β) or the same patch at a different time (temporal β), then we calculate

$$\beta = 1 - \frac{|A \cap B|}{|A \cup B|}.$$

2.4.4 | Quantifying invasibility

Quantifying α and γ is straightforward; we identify which species are present within patches and within the overall system. Quantifying invasibility is less clear. We quantify invasibility as the number of species in the pool that could both establish in a patch (positive local per capita growth rate) and then subsequently survive the full community and dispersal dynamics for five times the inverse of the magnitude of the largest eigenvalue of the interaction matrix (which is the inverse of the rate of interactions and events and thus sets a natural time scale). The invasibility values reported in Figure 4 then correspond to the median invasibility of a patch (computed over all patches) at the end of the simulation.

3 | RESULTS

3.1 | Example runs

Figure 3 illustrates three runs with the same pool of species, same set of patch environments and precisely the same history of immigration and extirpation events (which does not guarantee the same history of successful establishments if the communities differ, e.g. due to dispersal). The only difference in parameters is the change in dispersal from no dispersal between patches (zero inter-patch mixing case), to 'medium' and full dispersal cases, in which some or nearly all of the abundance on a patch can have moved to an adjacent patch in a single time unit respectively. These example pools, environments and histories have been selected at random. The no-dispersal example has many transient species represented by short horizontal dashes in the panels of Figure 3a, most of which occur in only a small number of patches at any one time (yellow), whereas the high dispersal example shows a smaller number of species present in most patches (purple) for most of the simulation run (long dashes); medium dispersal is intermediate.

In these three example simulations, exactly the same species immigrated at exactly the same time. This means that all of the species that successfully established in at least one patch in the zero (between patch) dispersal scenario also arrived in the corresponding patch in the full dispersal simulation, but many of them failed to establish at all. The long purple horizontal lines in Figure 3a indicate communities with limited (temporal) turnover—either extinction or establishment of new species. The high dispersal simulation generates communities that are robust to further invasion and successful

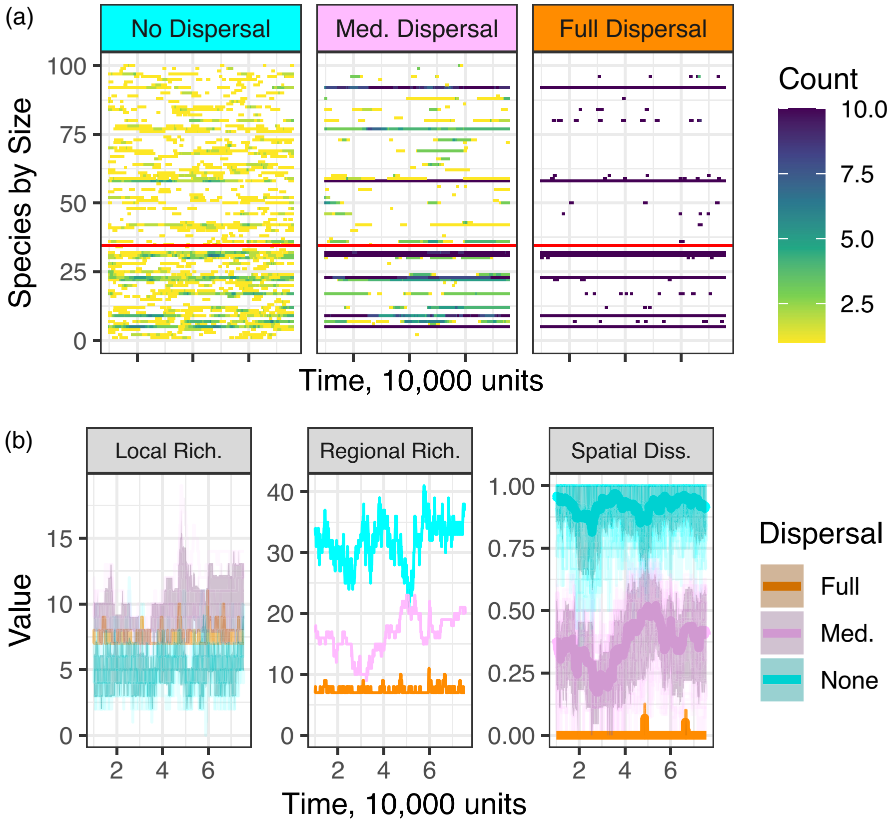

FIGURE 3 Three example simulation runs. Patch outcomes differ greatly dependent on the amount of dispersal permitted between the heterogeneous patches. Each simulation had the same neutral immigration and neutral extirpation history of 9370 events, and the same set of patch dynamics, but different dispersal rates (burnt-in for the first 10,000 time units prior to extracting results). Panels (a) show the occurrence of species, with horizontal lines indicating species identities, the duration of their presences in the patch network, and the number of patches they were present in ('count' colour shading) for the three dispersal rates (no dispersal: 0 dispersal rate, med.: 2×10^{-5}, full: 0.86). Species are ranked by size, with the horizontal red lines separating basal species (below) and consumer species (above the red lines). Panels (b) show the resulting local richness as the number of species per patch through time, the regional richness as the total number of species in the network and the extent to which species were shared among patches or communities contained different species in each patch at a given time as Jaccard dissimilarity index values near 0 or 1 respectively. The dark regions in the local richness (among 10 individual patches) and spatial dissimilarity plots (in pairwise comparisons between patches) correspond to 80% intervals, whereas there is only a single value for the total number of species present in the entire metacommunity at a given time (lower middle panel).

across heterogeneous environments once established, whereas immigrants are more likely to establish in isolated (no dispersal) communities. When patches are homogeneous, even medium levels of dispersal are sufficient to generate high community stability and uniformity (i.e. they look like the high dispersal scenario in heterogeneous environments), shown in Figure 4. Furthermore, the time series of events, that is, the colonisations, extinctions and extirpations, at both regional and local scales show clear evidence of temporal clustering, potentially indicative of cascades of change, and this clustering increases as dispersal does (see Figure S9). However, the increase in clustering with dispersal is primarily generated by some species establishing temporarily in otherwise robust communities, uninterrupted by other species (establishments followed by extinction of the same species; Figure 3a). Hence, these are not 'true' cascades in which establishment would lead to increased rates of establishment and extirpation by *other* species thereafter.

These dynamics result in low species richness on patches in the zero dispersal example but a large regional total number of species because the species present differ among patches due to environmental heterogeneity and local extirpation (high spatial dissimilarity; Figure 3). In contrast, full mixing generates higher local richness, but lower regional richness because the species are shared (low Jaccard values) among patches. While medium dispersal generates intermediate regional richness and dissimilarities among islands, it has the highest richness per island (Figure 3, bottom-left panel), supporting the hypothesis that intermediate dispersal can result in the highest levels of local diversity. Dispersal is the primary driver of trends; similar plots can be constructed for the varying immigration and extirpation rates, see Figures S3–S8.

3.2 | Metasimulation study

To investigate the influence of dispersal (mixing rate) and patch heterogeneity on local richness and regional richness, we conducted a large family of simulations in which we varied the dispersal rate,

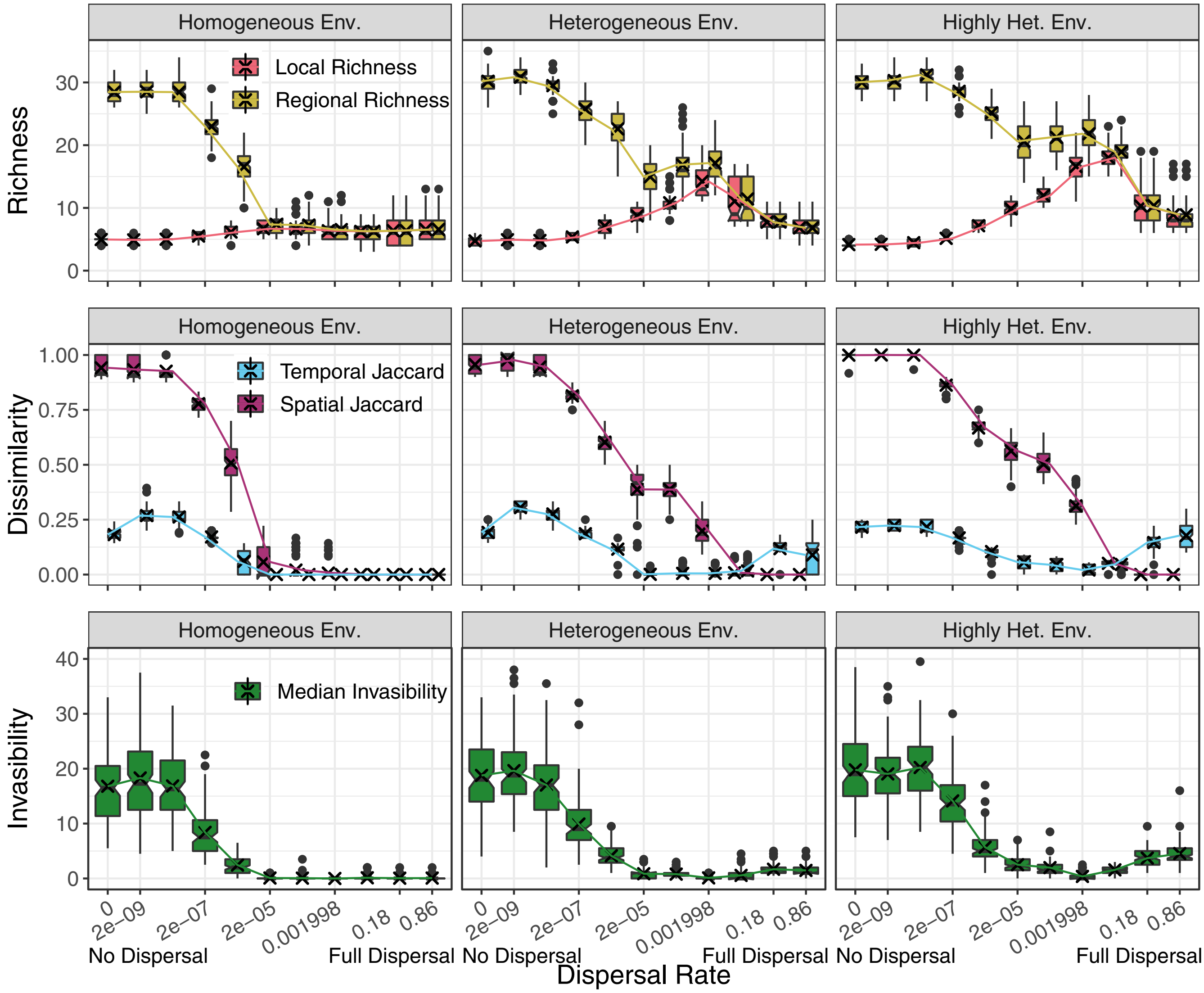

FIGURE 4 Metasimulation results for different biodiversity measures. The species richness (top row), community dissimilarity (middle row) and invasibility (bottom row) of communities vary with the dispersal rate, but are nuanced by the amount of heterogeneity between environments (homogeneous, heterogeneous or highly heterogeneous (left to right columns)); dispersal increases from left to right within each panel (proportions of individuals mixed between adjacent patches per time interval), covering the range from flightless sedentary organisms to true migrants. Colours indicate: local richness (top, red), regional richness (top, yellow), differences in community composition between patches (spatial Jaccard dissimilarity, magenta), how much community composition changes over time within patches (temporal Jaccard dissimilarity, blue), and invasibility (bottom, green) of the region at the end of the simulation with respect to the species pool. Each box and whisker plot is composed of a single median estimate of the corresponding metric from each of the 3300 simulations, see Section 2. Each cross represents the means of the each box-and-whisker plot, and the lines connect the crosses.

neutral immigration rate, neutral extirpation rate, pool structure and the presence of noise in the interaction matrices. See Tables S1–S3 in the Supplemental Information for details on parameter variations.

Figure 4 represents the overall relationship across 3300 simulations between dispersal rate and our measures of diversity, ecological differentiation (temporal turnover and spatial community dissimilarity) and the resistance of the 'end of simulation' communities to subsequent invasion from the mainland species pool. Additional simulation results are shown in the supplemental information, Figures S11 and S12. The relationship described in the three examples holds in general. Local richness (Figure 4 top row, red; the number of species per patch) peaks at intermediate dispersal rates, although barely when patch environments are homogeneous, confirming this hypothesis, while regional richness appears to reduce with increasing dispersal rates (top row, yellow). Broadly then, local and regional richness show opposing trends with increasing dispersal, until one reaches very high dispersal, when both local and regional richness values decline. The latter likely arises if species suited to particular patches, which differ somewhat in environmental conditions in the heterogeneous and highly heterogeneous cases, may be swamped out in runs with full dispersal. These results are robust to variations in pool parameters and immigration and extirpation rates (Figures S11 and S12).

Measures of beta diversity (Jaccard dissimilarity) over both space (magenta) and time (blue) are similarly sensitive to dispersal rates (Figure 4, middle row). Spatial Jaccard falls as the dispersal rate increases, indicating that high dispersal homogenises communities, as might be expected, and seen in the three example runs (Figure 3).

Temporal Jaccard indicates the extent to which the species composition on patches changes through time. This reveals relatively high turnover in the lowest dispersal systems, indicating a greater capacity of immigrants from the mainland pool to establish on otherwise unconnected patches, suggesting that dispersal among patches increases resilience. Temporal turnover reaches a minimum at intermediate dispersal rates—approximately where local richness peaks—before increasing just as local richness is falling (unless patch environments are homogeneous, Figure 4, left column). This arises in the simulations because new immigrants arrive in a single patch and quickly disperse to establish in the best (due to environmental variation among patches) patch for them, only to continue dispersing away more quickly than they can grow in abundance. The effect is related to source–sink dynamics and harvesting: population sources cannot persist if survivors cannot sustain the drain of lost (emigrant, harvested) individuals. It is only seen clearly when a substantial fraction of the total abundance of each species is redistributed among patches per time step, so this will be rare even in human-modified communities.

At the end of the simulations, we 'challenged' each patch community with species that exist in the mainland pool but that were not present in the archipelago to evaluate their resistance to further 'invasion' (Fitzgerald et al., 2016; Fridley & Sax, 2014; Moser et al., 2018). This revealed that low among-patch dispersal systems could be invaded much more easily than high dispersal systems. Taken together with the temporal Jaccard pattern of change, these results indicate that community networks become increasingly robust to subsequent invasion with increasing dispersal; more resilient (and commonly but not always more locally diverse) food webs are constructed from a larger pool of possible members. Invasibility and temporal turnover only diverge at the very highest, and least likely, dispersal levels, where source–sink dynamics between heterogeneous environments as well as species pool comes into play. Thus, the low invasibility and temporal turnover experienced by high dispersal systems makes it difficult to move them out of their equilibrium state.

These overall conclusions remain consistent across a range of different assumptions including varying the immigration rate, stochastic extirpation rate, removal of stochastic extirpations and the lower and upper limits of species sizes see Figures S3–S8, S11 and S12. Additionally, while our computational implementation of extirpation involves the random removal of a local population, the results are robust to changes to this assumption. For example, simulations where extirpation removes only 90% of a population show the same trends in the relationship between richness and dispersal (not shown). Varying dispersal consistently generates the overall shapes of the curves in Figure 4. Invasibility also increases with stochastic extinction, especially in low dispersal metacommunities. These communities lack particular components within their food webs, which in turn allows invasion. Since real island communities often lack particular functional components, for example, either because of failed colonisation or past extinction, and are susceptible to invasion, the increase in invasibility with reduced dispersal appears realistic.

4 | DISCUSSION

Our metacommunity model results indicate that increasing the rate of dispersal between ecological communities (patches, islands) produces trade-offs between different aspects of diversity. Local diversity (the number of species per patch, or alpha diversity) typically peaks at intermediate dispersal, while increasing dispersal drives declines in the distinctiveness of ecological communities (Jaccard dissimilarity, beta diversity). Consequently, the total number of species in the system (regional or total diversity, gamma diversity) mainly declines with increasing dispersal, although the intensity of the peak and fall depend on the amount of heterogeneity between environments. Since environments are never completely homogeneous among patches or islands, we expect the intermediate dispersal peak to be present in most if not all empirical systems. Colonisation and extirpation events are temporally clustered by community cascades as food webs reorganise, but communities experiencing higher dispersal rates became robust to further invasion. Hence, increases and decreases in just one process—dispersal—generates a variety of community dynamics and changes in measures of diversity. There is no universally 'best' level of dispersal or diversity metric (Whittaker, 1960), nor do they behave in the same way as one another, as might be wished in the context of biodiversity indicators and global biodiversity policy development (McGill et al., 2015).

In terms of biological invasions, our results provide similar context-dependent insights into the 'invasion debate' (Briggs, 2017; Davis, 2009; Davis et al., 2011; Russell & Blackburn, 2017). The model simulations exhibit emergent series of temporally correlated events (establishments, extirpations; though often arrivals followed by disappearance of the same species) consistent with narratives of community cascades (Simberloff, 2010) and the extinction of endemic species when previously isolated communities experience increased immigration (e.g. Sax & Gaines, 2008; Williamson, 1989). Nearly all IUCN-listed threatened species that are endangered by invasive (i.e. not previously present) species are in previously isolated communities: island communities for reptiles, birds, mammals and plants; and 'island-like' wetland environments within continents for freshwater fish and amphibians (Dueñas et al., 2021). In contrast, many other 'natural' ecosystems in continental regions, which have had higher background immigration rates, appear relatively robust to invasion, compared to human-altered ecosystems (which may still be in the 'burn-in period') (e.g. MacDougall & Turkington, 2005; Shimoji et al., 2022).

In the context of biodiversity trends, these results provide an opportunity to address the apparent disagreement between studies highlighting declines in biodiversity and studies highlighting variable but no-net decline trends. Although humans have altered ecological communities in many different ways, altered rates of dispersal are a common consequence. This frequently results in a more well-mixed world. The establishment of 'non-native' species is accelerating globally (Seebens et al., 2017). Equally, 'native' species are increasingly moving: range boundaries generally are shifting polewards and to higher elevations and deeper depths in response to anthropogenic climate change (e.g. Chen et al., 2011; Pecl et al., 2017; Sorte et al., 2010), such that species are colonising ecological communities from which they were previously absent at unprecedented rates. In contrast, metapopulation ecology has shown that dispersal/colonisation rates of habitat-specific species declines with habitat isolation, for example., from habitat fragmentation (Hanski, 1999), although the establishment rates of edge- and disturbance-related species may increase (Laurance et al., 2011).

Taken together, these results mean that the expected outcome in recent biodiversity monitoring is context dependent. It depends on the measure(s) of diversity change (as above), how isolated a community was prior to human intervention, that is, isolated island communities have experienced most extinctions associated with 'non-native' species, whether dispersal rates have increased or decreased in relation to local environmental changes, how different the local environments are, and the types of species considered. For example, in real ecosystems, habitat core and edge species may experience opposite changes to their dispersal rates associated with their abilities to move through human-modified environments, but many studies focus on core species. Species have different likelihoods of being transported by humans, and the natural dispersal rates of different taxonomic groups vary over many orders of magnitude while many studies are of only one or a few groups. Hence, different taxa may show different diversity trends even for identical sites. A combination of these factors should contribute to the debate over exactly what biodiversity trends exist.

As a caveat, it is important to recognise that our modelling framework only contains a subset of possible processes and assumptions. For example, we have focused on a single +/– species interaction type [exploitation (Cohen et al., 1993; Law & Morton, 1996; Morton & Law, 1997)]. Our justification for this is that the resulting network of interactions does permit the emergence of net –/– interactions via shared prey (resource mediated competition; but does not model interference competition) and shared predators (apparent competition), and net +/+ tritrophic and other indirect interactions can arise, as in real food webs. Our deterministic modelling framework does not include local (patch) or regional (network) stochastic or directional (e.g. mimicking climate change) temporal variation in the patch environments themselves, either. However, our code and pseudocode are freely available (see Data Availability Statement and Supplementary Information), so our model could be adapted or extended to examine outcomes when varying these and other assumptions. Future work would also benefit from explicit consideration of the implications of evolution (e.g. Govaert et al., 2021). While it would be valuable to explore additional processes, the model outputs reported nonetheless consistently provide clear evidence of the importance of dispersal and spatial heterogeneity for the diversity and invasion debates.

In conclusion, this simulation study has proposed one simple mechanism, dispersal relative to spatial scale, that has the capacity to connect the literature on the decline of global biodiversity, on how local biodiversity can remain relatively stable on average, and on how isolated ecological communities experience reorganisation (including extinctions but also increased community-level diversity) when experiencing recently increased immigration rates. While we find that dispersal is sufficient to explain different sides of the diversity and invasion debates, dispersal also interacts with many other temporal changes to the environment and these pressures should be considered together in any discussion of policy options. Whether people wish to manipulate or control dispersal rates will depend on which components of diversity and community invasibility, as well as functional processes, are prioritised in a given context.

AUTHOR CONTRIBUTIONS

All authors participated in conceptualisation. Brennen Fagan, Jon W. Pitchford and Susan Stepney contributed mathematical and coding methodology. Brennen Fagan created and conducted the simulations and performed formal analysis. Brennen Fagan and Chris D. Thomas wrote the manuscript. All authors reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All code, random seeds, R scripts and summarised data used to generate the simulations and subsequent figures are available in Zenodo and Github at https://doi.org/10.5281/zenodo.8314911 (Fagan, 2023). The >10TB of data generated from the code, random seeds and R scripts are available by request from the corresponding author.

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SUPPORTING INFORMATION

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