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Connecting local and regional scales with stochastic metacommunity models: Competition, ecological drift, and dispersal

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Abstract

Despite the well known scale-dependency of ecological interactions, relatively little attention has been paid to understanding the dynamic interplay between various spatial scales. This is especially notable in metacommunity theory, where births and deaths dominate dynamics within patches (the local scale), and dispersal and environmental stochasticity dominate dynamics between patches (the regional scale). By considering the interplay of local and regional scales in metacommunities, the fundamental processes of community ecology—selection, drift, and dispersal—can be unified into a single theoretical framework. Here, we analyze three related spatial models that build on the classic two-species Lotka–Volterra competition model. Two open-system models focus on a single patch coupled to a larger fixed landscape by dispersal. The first is deterministic, while the second adds demographic stochasticity to allow ecological drift. Finally, the third model is a true metacommunity model with dispersal between a large number of local patches, which allows feedback between local and regional scales and captures the well studied metacommunity paradigms as special cases. Unlike previous simulation models, our metacommunity model allows the numerical calculation of equilibria and invasion criteria to precisely determine the outcome of competition at the regional scale. We show that both dispersal and stochasticity can lead to regional outcomes that are different than predicted by the classic Lotka–Volterra competition model. Regional exclusion can occur when the nonspatial model predicts coexistence or founder control, due to ecological drift or asymmetric stochastic switching between basins of attraction, respectively. Regional coexistence can result from local coexistence mechanisms or through competition-colonization or successional-niche trade-offs. Larger dispersal rates are typically competitively advantageous, except in the case of local founder control, which can favor intermediate dispersal rates. Broadly, our models demonstrate the importance of feedback between local and regional scales in competitive metacommunities and provide a unifying framework for understanding how selection, drift, and dispersal jointly shape ecological communities.

KEYWORDS
coexistence, competition-colonization trade-off, Lotka–Volterra competition, metacommunity theory, priority effect, spatial structure, stochasticity

INTRODUCTION

Ecological communities are shaped by the fundamental processes of selection, drift, and dispersal (Vellend, 2010). Selection, which includes both niche and fitness differences (Chesson, 2000), has been the focus of much ecological theory. It is exemplified by the Lotka–Volterra competition model (Lotka, 1932; Volterra, 1926), ecology's most iconic model of interspecific competition. For almost a century, the Lotka–Volterra equations have provided the cornerstone of understanding competitive interactions between species; the Web of Science lists more than 1500 articles that mention "Lotka–Volterra competition" in their title, abstract, or keywords. The model is simple enough for analytical results, yet predicts diverse competitive outcomes (competitive exclusion, coexistence, and founder control) (Hofbauer & Sigmund, 1998).

More recently, however, this emphasis on local, deterministic processes has been increasingly challenged (Lawton, 1999). The most striking example is neutral theory, which is based on stochastic ecological drift and dispersal, but neglects selection (Hubbell, 2001). Given its simplicity, neutral theory does surprisingly well at predicting various macroecological patterns such as species abundance distributions and species area curves (Allouche & Kadmon, 2009; Chisholm & Pacala, 2010; Haegeman & Etienne, 2011; Hubbell, 2001; Rosindell et al., 2012). Yet species differ in ecologically relevant ways (Harpole & Tilman, 2006), in disagreement with the central assumption of neutrality. Only by tying together the fundamental processes of selection, drift, and dispersal can we ultimately achieve a complete picture of ecological communities (Cadotte, 2007; Gravel et al., 2006; Holt, 2006; Scheffer & van Nes, 2006).

Metacommunity ecology provides a multiscale framework for integrating selection, ecological drift, and dispersal in patchy landscapes (Holyoak et al., 2005; Leibold & Chase, 2017; Leibold et al., 2004). It was originally conceptualized as an organizing framework with four major paradigms (i.e., clusters of similar models; Leibold et al., 2004). At intermediate dispersal rates, the species-sorting paradigm corresponds to traditional community ecology, where local selective processes dominate. Under dispersal limitation, the patch-dynamics paradigm assumes that local population dynamics are fast relative to dispersal and disturbances, so that each patch can be assumed to be at equilibrium (although possibly invasible), and only the identities of the species present must be tracked (Klausmeier & Tilman, 2002). With dispersal surplus, the mass-effects paradigm invokes source-sink dynamics to explain the persistence of species that would otherwise be excluded (Koffel et al., 2022; Pulliam, 1988). Finally, ecological drift has largely been relegated to the neutral-theory paradigm, despite the general importance of stochasticity in community ecology (Shoemaker et al., 2020).

While these paradigms have been useful for organizing our understanding of metacommunities, they are based on different simplifying assumptions, use different mathematical formalisms, and even track different state variables (patch occupancy vs. species abundance), all of which impede their conceptual unification. Consequently, many now believe that metacommunity ecology must move beyond these special cases toward a unified framework that encompasses all of these paradigms (Brown et al., 2017; Leibold & Chase, 2017; Shoemaker & Melbourne, 2016; Thompson et al., 2020). A major step in the development of a unified metacommunity framework was taken by Thompson et al. (2020). They developed a multispecies, spatially explicit, simulation model of competitive metacommunities that captures the four paradigms as special cases and focuses their results on explaining how species' niches and dispersal rates shape patterns of various diversity measures (e.g., α, β, and γ). However, due to the complexity of such models, gaining detailed insight into the mechanisms that engender the different outcomes is difficult.

Our goal in this paper is to build toward a unified metacommunity model from a complementary angle. Community ecology is notoriously complex (Lawton, 1999; Simberloff, 2004). Simple models can help to cut through this complexity to obtain general insights. Rather than relying on complex simulations, our aim is to develop the simplest possible model that incorporates selection, drift, and dispersal.

To understand our full metacommunity model and provide clarity to the roles of dispersal and demographic stochasticity in shaping metacommunity dynamics, we investigate increasingly complex models. We start by reviewing the basics of the classic deterministic Lotka–Volterra competition model. We then turn it into an open system by incorporating dispersal with a regional species pool and examine how the qualitatively distinct outcomes of classic Lotka–Volterra competition (competitive exclusion, coexistence, founder control, and neutrality) are affected by dispersal. We further extend our model by incorporating stochasticity, where the stochastic Lotka–Volterra competition model originally suggested by Chiang (1954) serves as our starting point. More recently, immigration from the regional species pool was added to this single-patch model (Capitán et al., 2015, 2017; Haegeman & Loreau, 2011). Here, we examine this stochastic open-system model more thoroughly, across all local, deterministic qualitative outcomes and a range of dispersal rates. Finally, we couple an infinite number of such local patches together to derive a true multiscale metacommunity model. In this closed-metacommunity model, regional abundances are not fixed, but emerge from local dynamics coupled by dispersal; these regional abundances then provide feedback to influence local outcomes. This model exposes how selection, ecological drift, and dispersal interact to determine the outcome of metacommunity competition. We recover all of the classic metacommunity paradigms and coexistence mechanisms, but our framework generalizes these specific cases and provides a unified perspective on metacommunities.

CLASSIC LOTKA–VOLTERRA COMPETITION MODEL

The two-species Lotka–Volterra competition model has played a central role in theoretical ecology since its introduction (Hofbauer & Sigmund, 1998; Lotka, 1932; Volterra, 1926). As a deterministic nonspatial model, it represents pure selection sensu Vellend (2010). In this section, we summarize this model (henceforth referred to as the "classic LV competition model") and its behavior to provide a baseline for understanding the more general models incorporating dispersal and demographic stochasticity that we investigate in this paper.

The classic LV competition model is given by the following system of ordinary differential equations:

$$\begin{aligned}\frac{dN_1}{dt}&=r_1N_1\left(1-\frac{N_1+\alpha_{12}N_2}{K_1}\right)\\ \frac{dN_2}{dt}&=r_2N_2\left(1-\frac{N_2+\alpha_{21}N_1}{K_2}\right)\end{aligned}, \tag{1}$$

where N_i is the density of species i, r_i its intrinsic growth rate, and K_i its carrying capacity. The competition coefficients α_{ij} can be thought of as the competitive effect of species j on species i. Whenever $\alpha_{ij} > 1$, an individual of species j exerts a stronger competitive effect on species i than an individual of species i does on its own species. Note that other formulations of the classic LV competition model exist (Mallet, 2012). All parameters are assumed to be positive.

The classic LV competition model has four qualitatively different outcomes:

1. Competitive exclusion—species 1 outcompetes 2 ($K_1 > \alpha_{12}K_2$ and $K_2 < \alpha_{21}K_1$) or species 2 outcompetes 1 ($K_1 < \alpha_{12}K_2$ and $K_2 > \alpha_{21}K_1$).
2. Coexistence—species 1 and 2 coexist ($K_1 > \alpha_{12}K_2$ and $K_2 > \alpha_{21}K_1$).
3. Founder control—species 1 or 2 outcompetes the other depending on initial conditions ($K_1 < \alpha_{12}K_2$ and $K_2 < \alpha_{21}K_1$).
4. Neutrality—competitively equivalent species ($K_1 = \alpha_{12}K_2$ and $K_2 = \alpha_{21}K_1$).

For simplicity, we assume the two species have equal carrying capacities throughout unless otherwise noted. Under this assumption, we depict these four outcomes as a function of the competition coefficients α_{ij} in Figure 1.

DETERMINISTIC OPEN-SYSTEM MODEL

As our first extension of the classic LV competition model, we consider a local community in a single patch

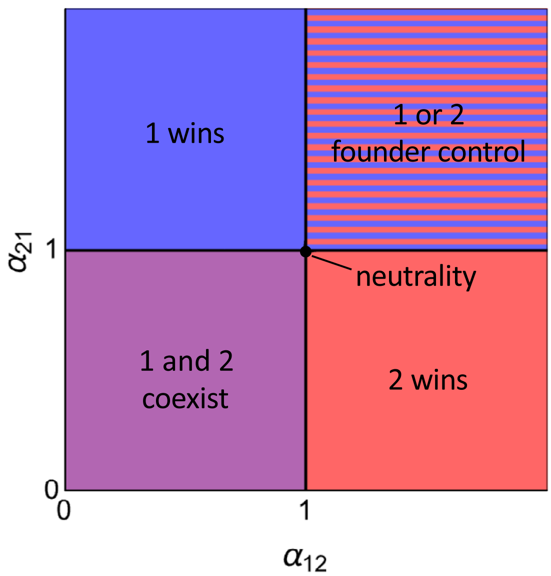

FIGURE 1 Outcomes in the classic (deterministic, local) Lotka–Volterra competition model (Equation 1), assuming equal carrying capacities ($K_1 = K_2$). Neutrality is at the intersection of the regions ($\alpha_{12} = \alpha_{21} = 1$).

that is open to dispersal from the external region, assuming fixed regional abundances. This type of model, also known as a mainland-island model (Hanski & Gyllenberg, 1993), could also represent a single patch in a metacommunity where the contribution of all the other patches is averaged over. The equations for this model extend the classic LV model (Equation 1) and are given by:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1\left(1-\frac{N_1+\alpha_{12}N_2}{K_1}\right)+m_1(N_{R,1}-N_1)\\ \frac{dN_2}{dt} &= r_2 N_2\left(1-\frac{N_2+\alpha_{21}N_1}{K_2}\right)+m_2(N_{R,2}-N_2).\end{aligned} \tag{2}$$

Here, m_1 and m_2 are the dispersal rates to and from the region of species 1 and 2, respectively, and $N_{R,1}$ and $N_{R,2}$ are the average regional abundances of species 1 and 2, respectively (Koffel et al., 2022). As with the classic LV equations, we analyzed Equation (2) by solving for the equilibria, which for these equations we did numerically, as the analytical solutions are not informative even when available. See also Fenchel (1975) and Holt (1983) who considered immigration of one of the competing species.

The addition of immigration from the region makes true exclusion impossible in the deterministic open-system model, so both species 1 and species 2 will always be present in the steady-state community, albeit possibly at very low densities. This also means that the boundaries between the four qualitative outcomes for the classic LV model will no longer always be sharp. With low dispersal, competitive exclusion still occurs for all practical purposes, but as dispersal increases the local dynamics become increasingly irrelevant and the system becomes dominated by mass effects from the region (Figure 2). Even though neither species will ever be entirely excluded, we can still identify founder control by calculating when there are two stable equilibria for the system. With low dispersal, the deterministic open-system model is similar to the classic LV model, but as dispersal increases, one of these equilibria collides with the unstable equilibrium and disappears, leaving the system with a single stable equilibrium under sufficiently high dispersal (Figure 3) (Fenchel, 1975).

To better compare the deterministic open-system outcomes to the classic LV outcomes (and forthcoming results from stochastic models), we depict each outcome as a "square-pie chart," where the size of each wedge gives the relative size of the basin of attraction of that equilibrium and its color indicates the relative abundances (see the legend for Figure 4). We then plot these outcomes along varying competitive abilities, for three different levels of dispersal (Figure 4; analysis described in Appendix S1). The figure thus shows the effective competitive exclusion of species 1 (2) as red (blue) squares, and coexistence as red-purple to purple to blue-purple squares as the relative density of species 1 increases at the coexistence point. Founder control is shown as a square with two wedges of different colors.

Figure 4 shows that the classic LV coexistence region is preserved when dispersal is added, although the boundary is blurred and, that for large dispersal rates, the coexistence region expands into the classic competitive-exclusion and founder-control regions (Figure 4a). Finally, with the addition of dispersal, the case of competitively identical species, $\alpha_{12} = \alpha_{21} = 1$, no longer holds any particular significance: the degenerate outcome of neutrally stable equilibria of the classic LV model is replaced by a single stable equilibrium (Fenchel, 1975). Although perhaps unsurprising, these results will serve as an important basis of comparison for our stochastic Lotka–Volterra models.

STOCHASTIC OPEN-SYSTEM MODEL

We now further extend the open-system Lotka–Volterra model by incorporating demographic stochasticity. We model the stochastic dynamics as a continuous-time Markov process (Renshaw, 2011). Unlike the continuous-state classic LV and deterministic open-system model, population sizes N_1 and N_2 now take on nonnegative integer values, representing the discrete nature of individuals in finite communities.

Populations change due to five demographic processes that occur at rates determined by the state of the system (Figure 5). A process that happens at rate Z will occur in a small time interval δt with probability $Z \times \delta t$ (Renshaw, 2011). The first two processes are a simple implementation of the local dynamics of the classic LV competition model:

1. Density-independent birth increases the population size of species i ($N_i \to N_i + 1$), at rate $B_i(N_i) = r_i N_i$.
2. Density-dependent death due to competition decreases the population size ($N_i \to N_i - 1$), at rate $D_i(N_1, N_2) = r_i N_i \left(N_i + \alpha_{ij} N_j\right)/K_i$, where j designates the other species, K_i is the carrying capacity of the focal species i and α_{ij} is the interspecific competition coefficient of species j on species i (intraspecific competition coefficients equal one in this formulation).

The next two processes model dispersal:

1. Immigration from the external region increases the population size ($N_i \to N_i + 1$), at rate $I_i = m_i N_{R,i}$,

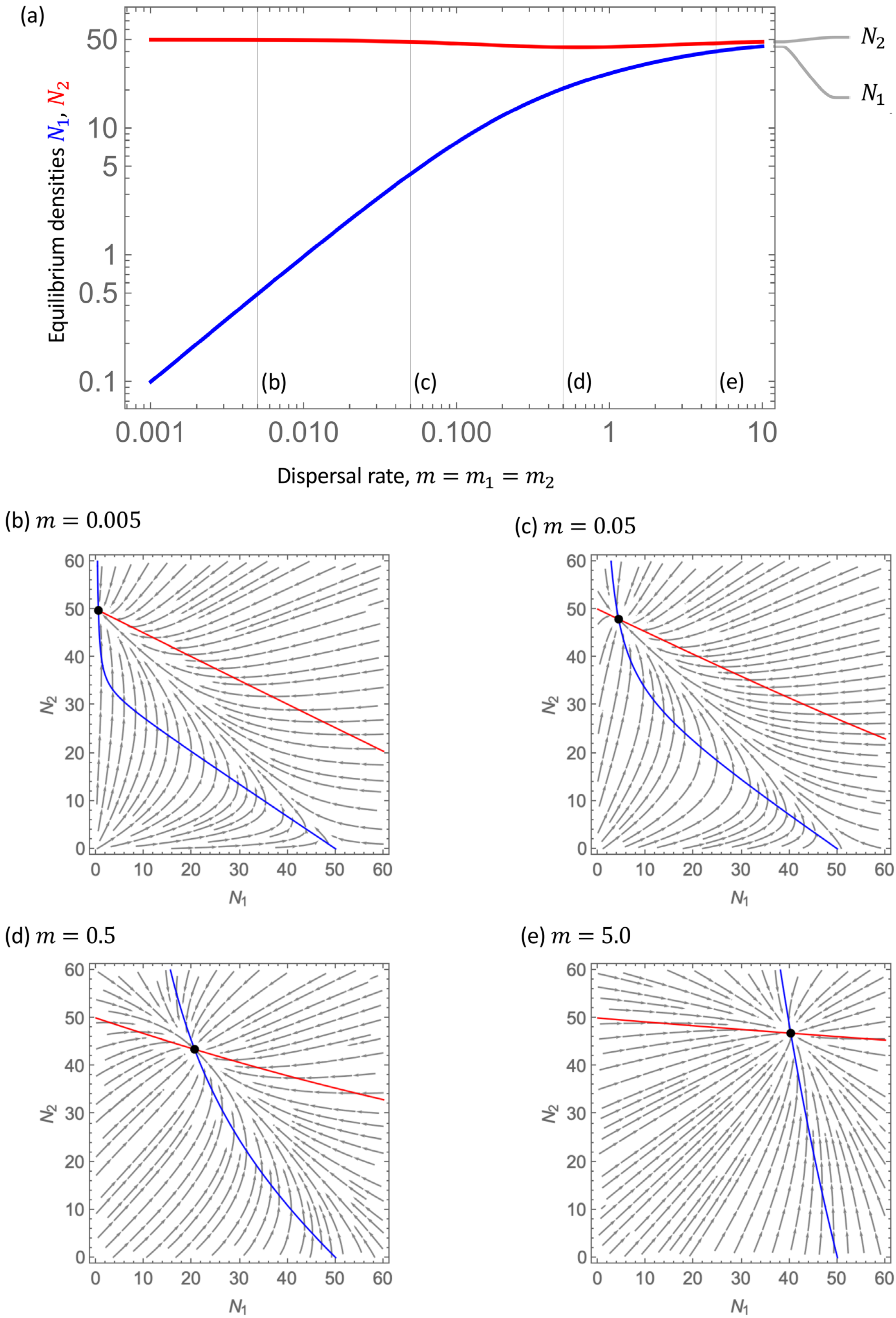

FIGURE 2 (a) Effective exclusion ($\alpha_{12} = 1.5, \alpha_{21} = 0.5$) then coexistence for increasing dispersal rate for the deterministic open-system model. (b–e) Phase planes for the levels of dispersal indicated in panel (a). Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$.

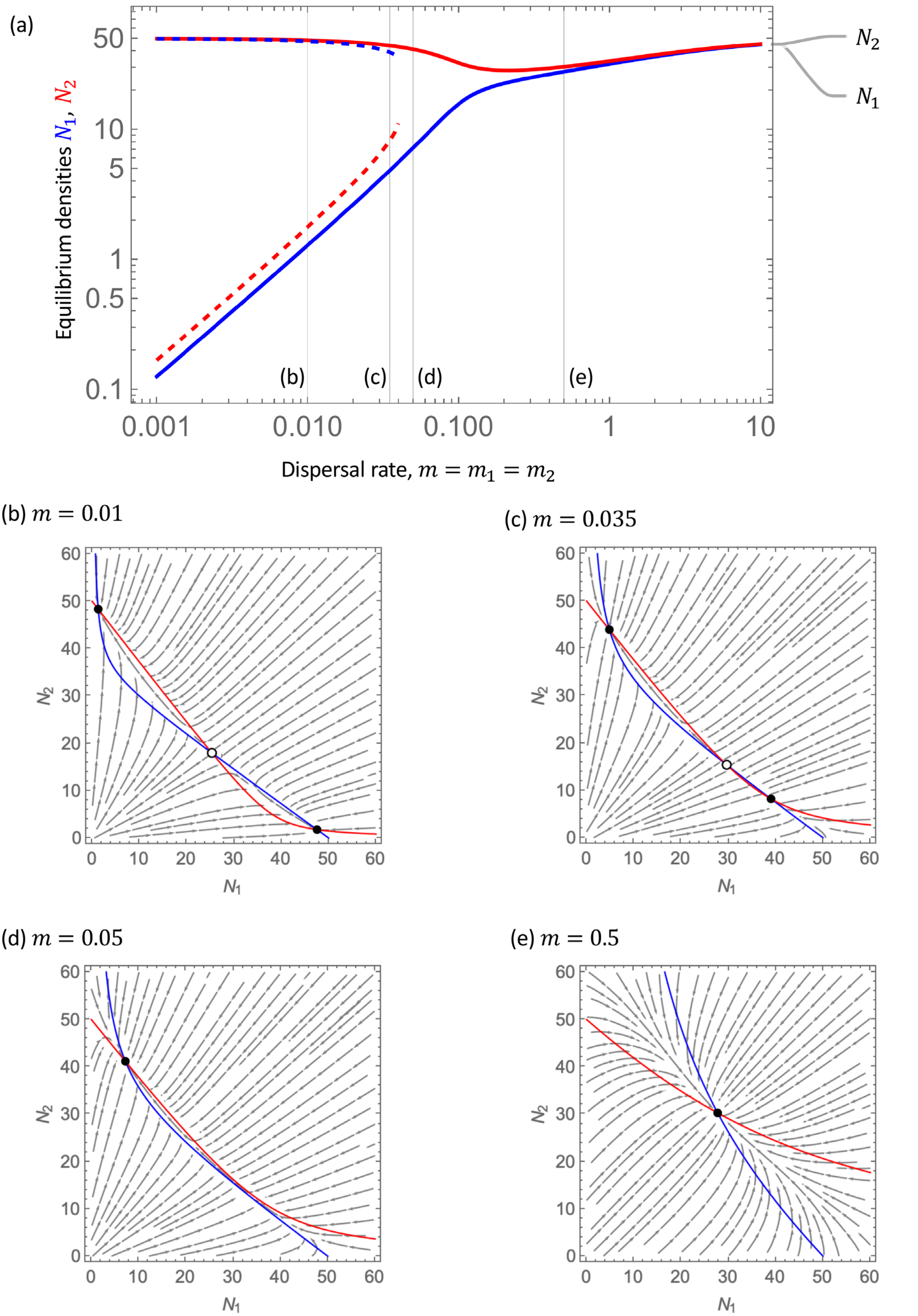

FIGURE 3 (a) Effective founder control ($\alpha_{12} = 1.4, \alpha_{21} = 1.3$) then coexistence for increasing dispersal rate for the deterministic open-system model. Solid lines depict one stable equilibrium, and dashed lines the other. (b–e) Phase planes for the levels of dispersal indicated in panel (a). Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$.

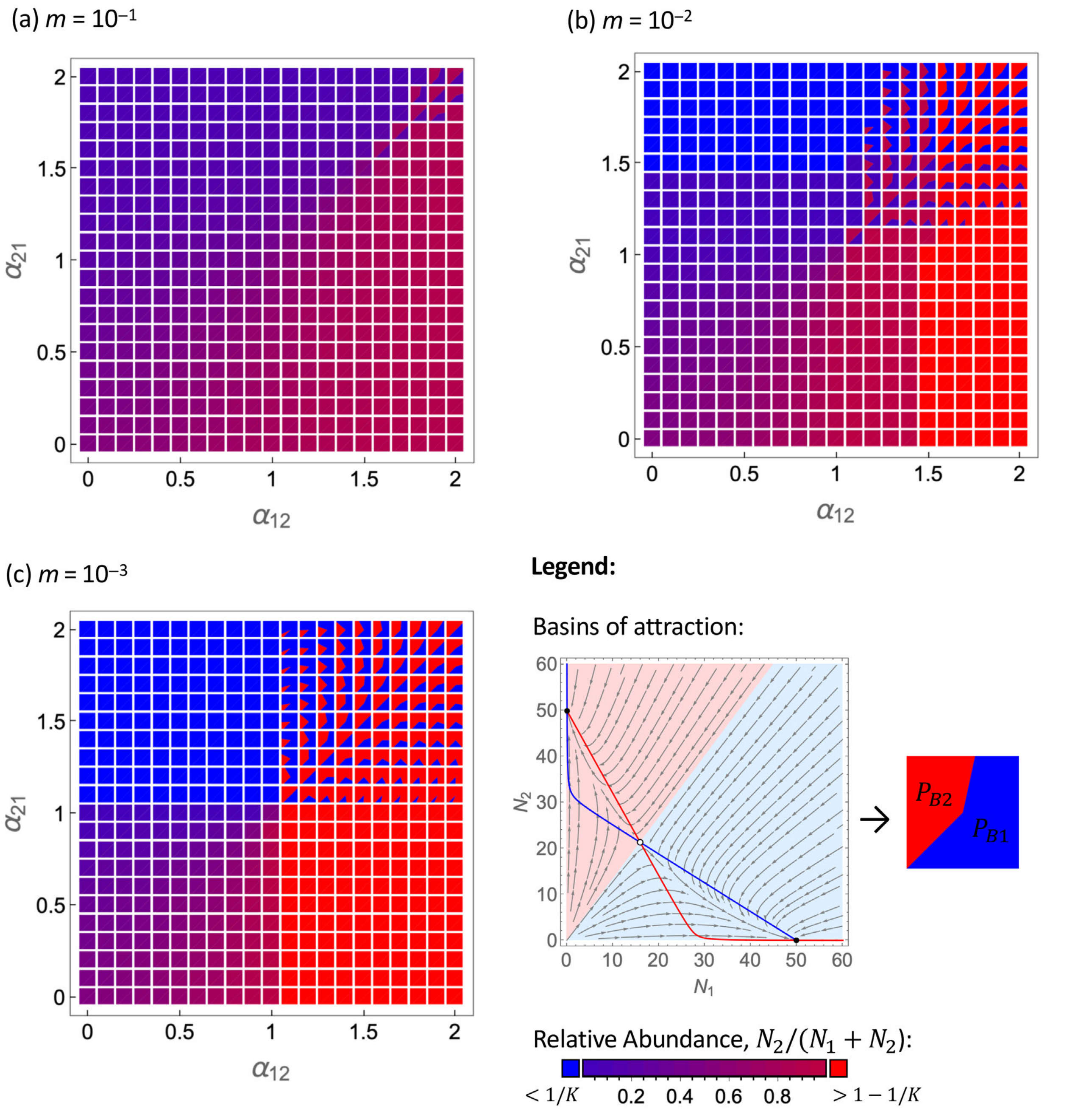

FIGURE 4 Summary of outcomes in the deterministic open-system model for decreasing equal ($m_1 = m_2 = m$) dispersal rates: (a) $m = 10^{-1}$ (b) $m = 10^{-2}$ (c) $m = 10^{-3}$. Phase portrait of Equation (2) with the two basins of attraction in blue and red. Shading indicates the relative abundance at equilibrium. The relative sizes of the basins P_{B1} and P_{B2} are used to make the square-pie charts. At high dispersal rates, both species persist at relatively high densities with a single stable equilibrium. Lower dispersal rates lead to bistability in the founder control region, and largely conform to the outcome without dispersal (Figure 1). Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$.

where m_i is the dispersal rate and $N_{R,i}$ is the fixed regional abundance of species i.

2. Emigration from the focal patch decreases the population size ($N_i \rightarrow N_i - 1$), at rate $E_i(N_i) = m_i N_i$.

The final process models external disturbances:

1. Disturbance drives both species to be locally extinct ($N_1 \rightarrow 0, N_2 \rightarrow 0$) at rate X.

Given the above demographic processes, the most straightforward means of analysis is to simulate the dynamics (Figures 6–8b,d,f). However, because these simulations are inherently noisy, obtaining clean results requires time-consuming simulations, even using the relatively efficient Gillespie algorithm (Gillespie, 1977; Renshaw, 2011). A more elegant approach is to model how the probability distribution of community states $P(N_1,N_2)$ changes over time, which is given by the

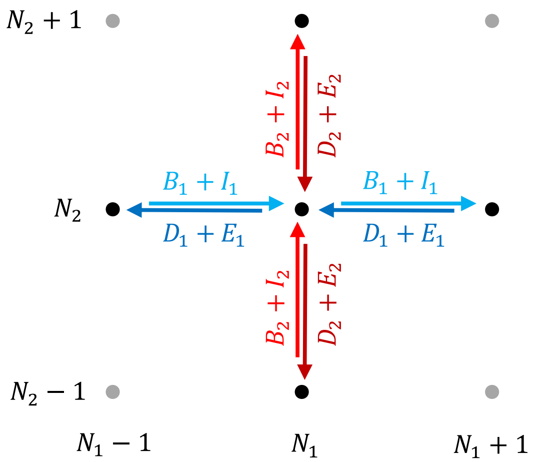

FIGURE 5 State transitions in the stochastic LV model.

"master equations" (Capitán et al., 2015; Chiang, 1954; Renshaw, 2011):

$$\begin{aligned}\frac{dP(N_1,N_2)}{dt} = {} & [B_1(N_1-1)+I_1(N_1-1)]P(N_1-1,N_2)\\ & +[B_2(N_2-1)+I_2(N_2-1)]P(N_1,N_2-1)\\ & +[D_1(N_1+1,N_2)+E_1(N_1+1)]P(N_1+1,N_2)\\ & +[D_2(N_1,N_2+1)+E_2(N_2+1)]P(N_1,N_2+1)\\ & -[B_1(N_1)+I_1(N_1)+D_1(N_1,N_2)+E_1(N_1)\\ & +B_2(N_2)+I_2(N_2)+D_2(N_1,N_2)\\ & +E_2(N_2)+X]P(N_1,N_2).\end{aligned} \tag{3}$$

Equation (3) explicitly tracks the changing probability distribution of population sizes driven by the transitions shown in Figure 5. For example, the first term accounts for births and immigration events of species 1, where one individual of species 1 is added to the patch (i.e., a (N_1-1,N_2) state transitions to a (N_1,N_2) state). Because probability mass is conserved, each process is featured twice, through a creation and a removal term (with all removals collected in the last term of Equation 3). Equation (3) is a doubly infinite set of equations from $0 \le N_1 < \infty, 0 \le N_2 < \infty$, but $P(N_1,N_2)$ is vanishingly small for sufficiently large N_i. Therefore, in practice, we truncate the system at the value $N_{\max}$ taken as twice the carrying capacity, which is large enough to ensure that there is a negligible probability of mass reaching the edge of our state space. Because Equation (3) is linear in the probabilities $P(N_1,N_2)$, it can be rewritten in compact vector–matrix form as $\frac{dP}{dt} = \mathrm{AP}$, with the transition-rate matrix A.

Stochastic open-system methods

While the master Equation (3) can be used to project the probability distribution of community states through time, we are often most interested in the system's long-term behavior. An extension to the Perron–Frobenius Theorem for real matrices that are nonnegative except along the diagonal guarantees the existence and uniqueness of the stationary distribution $\widehat{P}(N_1,N_2)$ (Virgo & Guttenberg, 2015). It is given by the eigenvector associated with the dominant, zero eigenvalue of the transition-rate matrix A, which can be efficiently calculated numerically. The stationary distribution $\widehat{P}(N_1,N_2)$ provides a detailed description of the long-term behavior of the system, but this level of detail can make it difficult to understand how species parameters affect the outcome. Therefore, following Capitán et al. (2015), we decompose the stationary distribution into discrete outcomes by identifying local peaks in probability $\left(\widehat{N}_1,\widehat{N}_2\right)$ where the community spends considerable time, which roughly correspond to equilibria of the deterministic system (Equation 2). We then sum the probability distribution in the basin of attraction of each peak to summarize the overall probability distribution as the probability of being associated with a given outcome to obtain more-readily interpreted values. As we did for the deterministic open-system model, we summarize these coarse-grained outcomes by a "square-pie chart," with the wedges color coded by the corresponding relative abundance of the species at the peak (insets in Figures 6–8a,c,e, and 9) and the size of the wedges representing the summed probability of each outcome.

Stochastic open-system results

In an isolated system ($m_i = 0$), the stationary distribution $\widehat{P}(N_1,N_2) = \begin{cases} 1, N_1 = 0, N_2 = 0 \\ 0, \text{otherwise} \end{cases}$ reflects the inevitable extinction of both species as a result of drift. However, in an open system ($m_i > 0$), the stationary distribution is always nontrivial due to constant, nonzero immigration rates. For this section, we omit disturbance ($X = 0$) to facilitate the comparison with the classic and deterministic open-system LV outcomes. We first give three examples whose competition coefficients result in three of the qualitative outcomes of the classic LV competition model: competitive exclusion, coexistence, and founder control.

Our example of classic LV competitive exclusion (Figure 6) largely follows the expected outcome of the

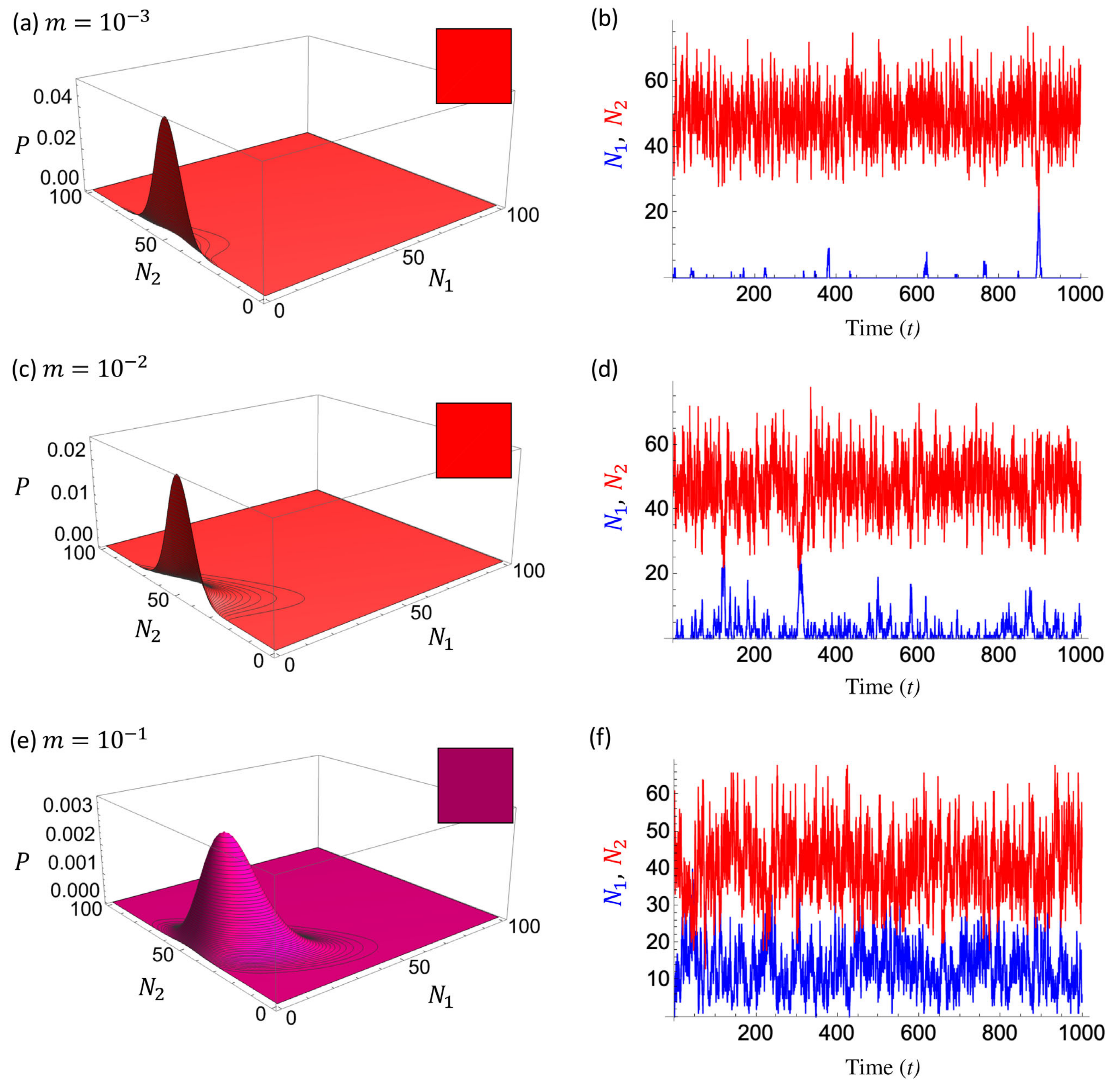

FIGURE 6 Example outcomes in the stochastic open system corresponding to competitive exclusion in the classic LV model ($\alpha_{12} = 1.25, \alpha_{21} = 0.8$) for increasing equal ($m_1 = m_2 = m$) dispersal rates: (a, b) $m = 10^{-3}$, (c, d) $m = 10^{-2}$, (e, f) $m = 10^{-1}$. (a, c, e) Stationary probability distribution $\widehat{P}(N_1, N_2)$, colored according to coarse-grained states as in Figure 9. (b, d, f) Example time series. At low dispersal rates the dominant competitor (species 2) can almost completely exclude the inferior competitor (species 1). However, the inferior competitor is maintained by mass effects given sufficient dispersal. Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$, $X = 0$.

corresponding deterministic, nonspatial model. Under low dispersal rates, the community is dominated by the superior competitor, with the inferior competitor often completely absent from the patch (Figure 6a,b). These intermittent extinctions could not occur in the deterministic open system, where any level of dispersal precluded exclusion. As dispersal increases, the inferior competitor, species 1, occurs more consistently and with increasing abundance in the patch, supported by mass effects from the region (Figure 6c–f).

In our example of classic LV coexistence (Figure 7), large dispersal rates lead to the expected outcome of coexistence, with approximately normally distributed variation around the equilibrium (Figure 7e,f). As dispersal becomes more limited (Figure 7a–d), the system spends more time in the vicinity of the two monoculture equilibria, with infrequent transitions between them

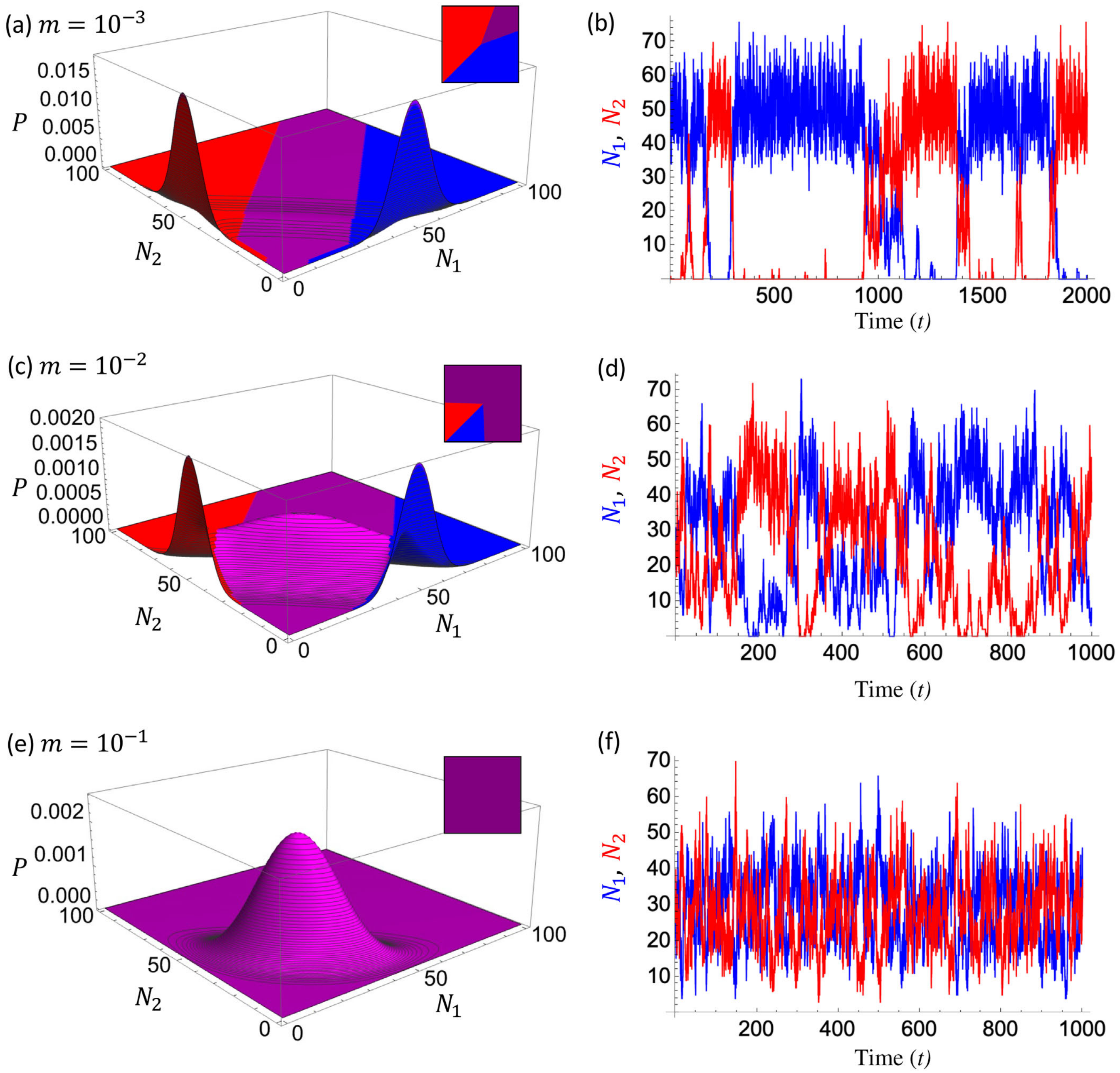

FIGURE 7 Example outcomes in the stochastic open system corresponding to coexistence in the classic LV model ($\alpha_{12} = \alpha_{21} = 0.9$) for increasing equal ($m_1 = m_2 = m$) dispersal rates: (a, b) $m = 10^{-3}$, (c, d) $m = 10^{-2}$, (e, f) $m = 10^{-1}$. (a, c, e) Stationary probability distribution $\widehat{P}(N_1,N_2)$, colored according to coarse-grained states as in Figure 9. (b, d, f) Example time series. Due to demographic stochasticity, both species rarely co-occur with low dispersal; however, both species almost always occupy the patch simultaneously with high dispersal. Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$, $X = 0$.

(Figure 7b,d), leading to trimodal probability distributions (Figure 7a,c), as first noted by Capitán et al. (2015). Thus, ecological drift overcomes the stable coexistence predicted by the corresponding deterministic model through frequent extinctions of single species, which are reversed when it successfully recolonizes from the regional landscape. Note that making interspecific competition weaker or making the carrying capacity larger (compared with $\alpha_{12} = \alpha_{21} = 0.9$ and $K_1 = K_2 = 50$ shown in Figure 7) would lead to the system spending less time close to the monoculture equilibria for a given dispersal rate.

Our example of classic LV founder control (Figure 8) is similar to that of deterministic coexistence (Figure 7) at high dispersal rates (apparent coexistence; Figure 8e,f) and low dispersal rates (with even more infrequent transitions between monoculture equilibria, Figure 8a,b). Intermediate dispersal rates illustrate a qualitatively new outcome: alternation between two

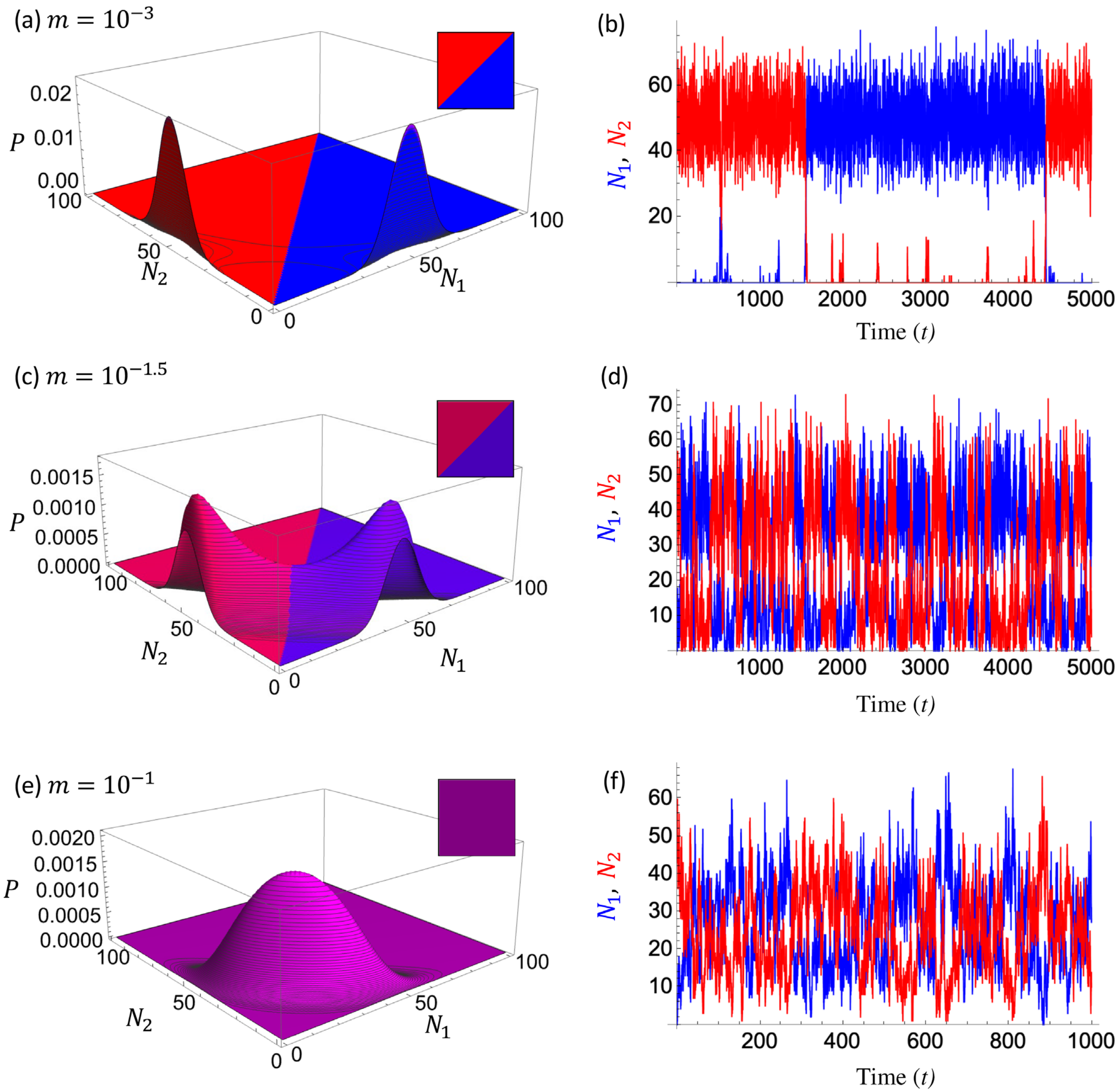

FIGURE 8 Example outcomes in the stochastic open system corresponding to founder control in the classic LV model ($\alpha_{12} = \alpha_{21} = 1.2$) for increasing equal ($m_1 = m_2 = m$) dispersal rates: (a, b) $m = 10^{-3}$, (c, d) $m = 10^{-1.5}$, (e, f) $m = 10^{-1}$. (a, c, e) Stationary probability distribution $\widehat{P}(N_1, N_2)$, colored according to coarse-grained states as in Figure 9. (b, d, f) Example time series. Given sufficiently high dispersal rates, both species coexist; otherwise, the probability distribution remains bimodal. Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$, $X = 0$.

alternative coexistence states with relative dominance by each species and the other maintained by mass effects (Figure 8c,d) as seen in the deterministic open system (Figure 3).

Figure 9 summarizes the coarse-grained outcomes as a function of the competition coefficients for three dispersal rates. As above, the stochastic model exhibits analogs of the classic LV model outcomes: (1) effective competitive exclusion ($\widehat{N}_1 > 0, \widehat{N}_2 \approx 0$—blue squares, $\widehat{N}_2 > 0, \widehat{N}_1 \approx 0$—red squares), (2) stable coexistence ($\widehat{N}_1 > 0, \widehat{N}_2 > 0$—purple squares), and (3) apparent founder control, with two peaks in the probability distribution corresponding to monoculture equilibria ($\widehat{N}_1 > 0, \widehat{N}_2 \approx 0$ and $\widehat{N}_2 > 0, \widehat{N}_1 \approx 0$—split blue/red squares, as Figure 8a,b) or alternating dominance by each species ($\widehat{N}_1 \gg \widehat{N}_2 > 0$ and $\widehat{N}_2 \gg \widehat{N}_1 > 0$, split blue-purple/

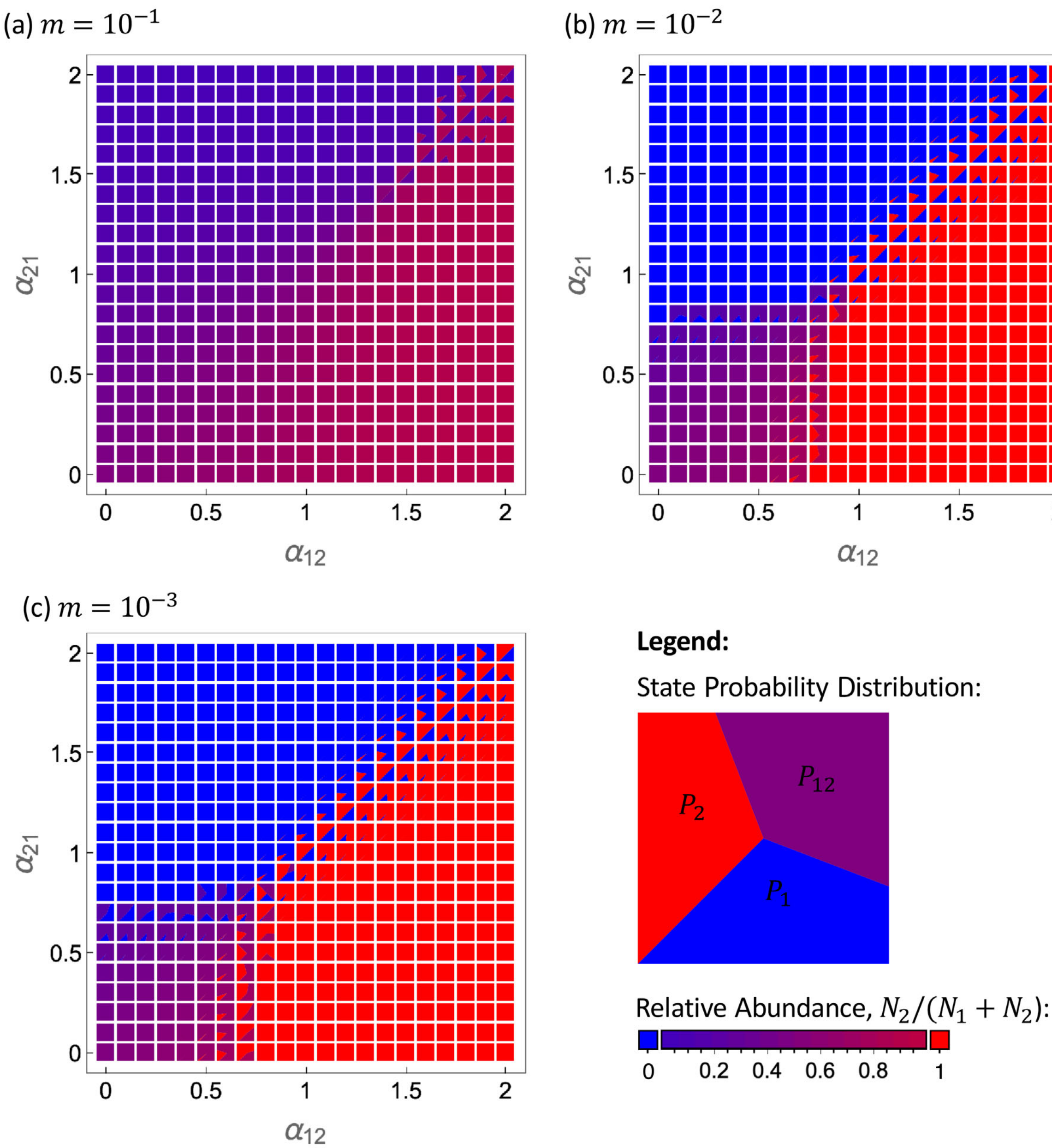

FIGURE 9 Summary of outcomes in the stochastic open system for decreasing equal ($m_1 = m_2 = m$) dispersal rates: (a) $m = 10^{-1}$, (b) $m = 10^{-2}$, (c) $m = 10^{-3}$. Each square represents the equilibrium distribution of patch types for a particular set of parameter values, as in Figures 6–8. With high dispersal rates, both species coexist. Decreasing dispersal rates lead to competitive exclusion with both the coexistence and (especially) founder control regions reduced compared to the classic LV model (Figure 1). Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = K = 50$, $N_{R,1} = N_{R,2} = K$, $X = 0$.

red-purple squares, as Figure 8c,d). The stochastic open system also shows trimodal outcomes (both monocultures plus coexistence states, as Figure 7c,d, split blue/red/purple squares; Capitán et al., 2015).

Comparing stochastic and deterministic open-system results

We can compare the outcomes for the stochastic open-system model (Figure 9) to the outcomes in the deterministic open-system model (Figure 4) to separate the influence of dispersal and stochasticity on Lotka–Volterra competition. For high dispersal rates, the outcomes in the deterministic and stochastic open systems are qualitatively similar (Figures 4a and 9a). Both models exhibit expanded coexistence regions and smaller founder-control regions in α_{12}–α_{21} space compared with the classic Lotka–Volterra model (Figure 1), as dispersal heavily subsidizes inferior competitors, making competitive exclusion more difficult.

For low dispersal however, the deterministic open-system model (Figure 4b,c) differs markedly from the stochastic open-system model (Figure 9b,c). The deterministic open-system model (Equation 2) approaches the classic Lotka–Volterra model (Equation 1), as one would expect, while the stochastic open-system model differs in two respects. First, the coexistence region for the stochastic open system is somewhat reduced, and second, the founder-control region is strongly reduced. While these two differences are both induced by stochasticity, as we explain below and in Appendix S2, two different mechanisms are responsible for the discrepancies. To understand these two mechanisms, we must delineate how the effects of stochasticity change with carrying capacity.

The deterministic open-system model is, in a sense, the large-population limit of the stochastic open-system model, as under very large populations, stochastic fluctuations become small compared with the size of the population. In Appendix S3: Figure S1, we depict the effects of increasing carrying capacity under low dispersal ($m=10^{-3}$). As the carrying capacity increases, the coexistence region approaches the coexistence region for the deterministic open-system model. Thus, the reduction of the coexistence region in the stochastic open-system model compared with the deterministic model is due to small population effects (ecological drift). Curiously, the founder-control region exhibits the opposite pattern as the carrying capacity increases, where the founder-control region becomes even smaller (Appendix S3: Figure S1). This occurs due to the asymmetry in the switching rates between the two basins of attraction for which species dominates a patch increases with carrying capacity (see Appendix S2 for details).

METACOMMUNITY MODEL

Although the open-system models may be applicable on shorter timescales and to mainland-island systems where regional abundances may be treated as constant, the feedback from local to regional dynamics cannot be neglected on longer timescales in metacommunities consisting of many local patches. In particular, explanations of species coexistence ultimately require a closed system that does not rely on immigration from outside the system (Chesson, 2000). At first thought, extending our stochastic open-system model to multiple patches may seem intractable due to the complexity of incorporating demographic stochasticity in even one patch (Equation 3). Fortunately, as we show below, a closed-metacommunity model can be derived with the same number of equations as the stochastic open-system model, $N_{\max}^2$. While this closed-metacommunity model is nonlinear, it is still possible to efficiently solve for equilibria numerically. Unlike the open-system models, species can now become extinct regionally. Thus, there are now multiple equilibria, corresponding to the empty system, monocultures of each species, and potential coexistence. Invasion criteria can also be calculated, allowing us to sharply delineate the different competitive outcomes at the regional metacommunity scale: competitive exclusion, coexistence, and founder control.

We assume an infinite number of patches that are identical in their underlying environmental conditions, but that vary in their population densities at any instant. We also assume that dispersal is global, connecting all patches to each other equally (a spatially implicit approach). We follow the dynamics of the probability distribution of community states $P(N_1,N_2)$ as in Equation (3). Due to ergodicity (Metz & Gyllenberg, 2001), this has two equivalent interpretations: as the probability distribution over time in a single patch and as the probability distribution over space across the metacommunity. The key insight is that the regional abundance $N_{R,i}$ of each species is no longer a free parameter, but reflects the mean abundance of that species averaged across the probability distribution $P(N_1,N_2)$:

$$N_{R,i}=\overline{N}_i=\sum_{(N_1,N_2)} P(N_1,N_2)N_{i.} \tag{4}$$

Substituting Equation (4) in the master Equation (3) yields our closed-metacommunity model.

Metacommunity model methods

As noted above, our closed-metacommunity model Equations (3) and (4) is a nonlinear system of $N_{\max}^2$ equations. Therefore, it is not analytically tractable and must be analyzed numerically. The most straightforward approach is to numerically integrate the dynamics over time. We use this method to study the dynamics of invasion, but it remains too slow to carefully explore parameter space.

An alternative approach is to focus on long-term outcomes by finding equilibria and their stability. Given the high dimensionality of the system, applying a numerical root-finding algorithm directly to Equations (3) and (4) with $\frac{dP}{dt}=0$ is slow and not guaranteed to converge. However, each species can be characterized by a single number, its average abundance $\overline{N}_i$, greatly reducing the dimensionality of the problem. We use the stochastic open-system model to construct a black-box function that outputs the average local abundance $\left(\overline{N}_1,\overline{N}_2\right)$ for a given regional-abundance $(N_{R,1}, N_{R,2})$ input. To efficiently find the metacommunity equilibrium, we apply a numerical root-finding algorithm to this black-box function to find $(\overline{N}_1, \overline{N}_2) = (N_{R,1}, N_{R,2})$, yielding a self-consistent solution (see Ghoshal et al., 2004; Metz & Gyllenberg, 2001 for similar approaches to different models).

We can also use this black-box function to calculate metacommunity-level invasion criteria. First, we find the species i monoculture equilibrium $\widehat{\overline{N}}_i$ by solving $(\overline{N}_i, \overline{N}_j) = (N_{R,i}, 0)$. Then, we introduce a vanishingly small inoculum ϵ of species j by setting $(N_{R,i}, N_{R,j}) = (\widehat{\overline{N}}_i, \epsilon)$ and calculating its average abundance $\overline{N}_j$. We define $\lambda_{j,i} \equiv \log(\overline{N}_j/\epsilon) > 0$ as the invasion criterion of species j into resident species i (see Casagrandi & Gatto, 2002; Massol et al., 2009, and Metz & Gyllenberg, 2001 for related approaches to metacommunity invasion criteria). These invasion criteria can be interpreted the usual way (Grainger et al., 2019; Turelli, 1978) to determine the outcome of competition at the regional metacommunity scale: if $\lambda_{1,2} > 0$ and $\lambda_{2,1} < 0$, species 1 excludes species 2; if $\lambda_{1,2} < 0$ and $\lambda_{2,1} > 0$, species 2 excludes species 1; if $\lambda_{1,2} > 0$ and $\lambda_{2,1} > 0$, species 1 and 2 coexist; and if $\lambda_{1,2} < 0$ and $\lambda_{2,1} < 0$, there is founder control. Boundaries between outcomes in parameter space can be determined numerically by setting $\lambda_{j,i} = 0$.

Metacommunity model results

We first look at the range of outcomes in the classical LV model by varying the competition coefficients α_{12} and α_{21} for a set of dispersal rates assumed to be equal ($m_1 = m_2 = m$) (Figure 10). For large dispersal rates, the outcome nearly matches that of the classic LV model (Figure 10a vs. Figure 1). Echoing the results of the stochastic open-system model (Figure 9), as dispersal becomes more limited, the regions of competitive exclusion expand at the expense of the coexistence and founder-control regions, with the founder-control region practically disappearing for $m < 10^{-3}$ (Figure 10b–d). Note that neutrality in the classic LV model ($\alpha_{12} = \alpha_{21} = 1$) leads to regional neutrality in this case of equal dispersal rates. Looking at the distribution of coarse-grained outcomes in cases of coexistence, we see that species are less likely to co-occur in a patch when interspecific competition is large (Appendix S3: Figure S2). Increasing the community size by increasing K enlarges the coexistence region, but has little effect on the founder-control region (Appendix S3: Figure S3), as explained for the stochastic open system above and in Appendix S2.

Next, we consider the impact of unequal dispersal rates (Figure 11), assuming symmetric competition ($\alpha_{12} = \alpha_{21} = \alpha$) across the range of outcomes in the classical LV model. In the case of coexistence in the classic LV model ($\alpha < 1$), species coexist at the metacommunity scale if neither species' dispersal rate is below a threshold value or if they have similar dispersal rates (Figure 11a,b). In the case of neutral competitors ($\alpha = 1$), stable coexistence at the metacommunity scale is impossible: the species with the higher dispersal rate excludes the other (Figure 11c).

The case of founder control in the classic LV model ($\alpha > 1$) is more complicated (Figure 11d–f). As seen in Figure 10, classic LV founder control never scales up to regional coexistence. Much like the case of classic LV coexistence, when both species have low dispersal rates, the better disperser outcompetes the other species at the metacommunity scale, since dispersal must be high enough for the invader to take over patches occupied by the resident species. However, continuing to increase dispersal rates leads to founder control at the metacommunity scale. This occurs because when dispersal rates are too high, the invader is unable to hold onto a patch, since individuals quickly disperse away. Thus, overall, an intermediate dispersal rate is best for a species to invade a monoculture of the other.

These local–regional feedback also alter the dynamics of the invasion process (Figure 12). Near the upper boundary of the region where species 1 wins ("x" marker in Figure 11e), the invasion accelerates over time, displaying faster-than-exponential dynamics (Figure 11b). This is the result of positive feedback between patches occupied and the takeover of new patches. As more patches become occupied regionally, the immigration rate increases, moving the boundary between local basins of attraction closer to the resident equilibria, which facilitates further stochastic transitions between states, accelerating the invasion process.

External disturbances ($X > 0$) have little effect on the outcome in the case of coexistence ($\alpha < 1$; Appendix S3: Figure S4a,b) or neutrality ($\alpha = 1$, Appendix S3: Figure S4c), but change the outcomes in the case of founder control in the classic LV model ($\alpha > 1$; Appendix S3: Figure S4d–f, compared with Figure 11). Disturbances increase the importance of colonizing empty patches, so that regions of parameter space that resulted in regional founder control in the absence of disturbances now result in competitive exclusion. The ability to colonize recently disturbed patches makes it easier for better colonizers to exclude poorer ones, a result that is mirrored in the case of a competition-colonization trade-off (see below).

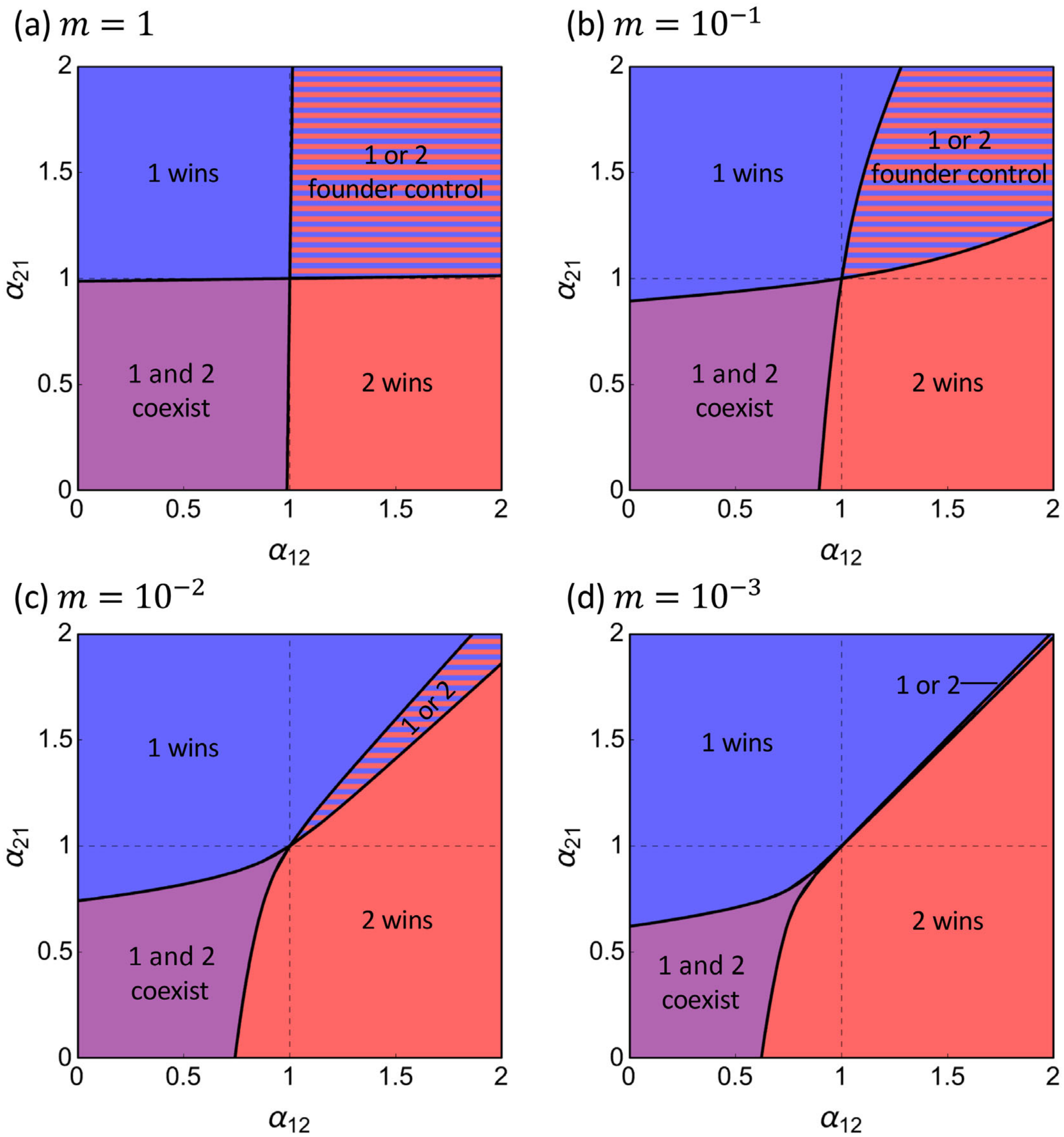

FIGURE 10 Outcomes in the metacommunity model for decreasing equal ($m_1 = m_2 = m$) dispersal rates: (a) $m = 1$, (b) $m = 10^{-1}$, (c) $m = 10^{-2}$, (d) $m = 10^{-3}$. High dispersal rates conform to the classic LV model. Both the coexistence and (especially) founder control regions shrink, and are replaced by competitive exclusion, with lower dispersal rates. Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = 50$, $X = 0$.

Finally, we consider two trade-offs that allow regional coexistence despite local competitive exclusion: the competition-colonization trade-off (Hastings, 1980; Hutchinson, 1951; Tilman, 1994) and the successional-niche trade-off (Pacala & Rees, 1998). In both cases, we assume that species 1 is the better local competitor.

A competition-colonization trade-off occurs when the inferior competitor has a higher dispersal rate ($m_2 > m_1$) (Figure 13). For a broad range of parameter values, there is regional coexistence, and for a narrow range at a high dispersal rate of species 2, regional founder control occurs (Figure 13a). Figure 13b,c shows the patch dynamics expected under competition-colonization coexistence: recently disturbed patches are rapidly colonized by species 2, which dominates until species 1 arrives and displaces it. Interestingly, for larger dispersal rates of species 2, it is not excluded when species 1 colonizes the patch but co-occurs locally due to mass effects (Figure 13d,e).

A successional-niche trade-off exists when the inferior competitor has a higher local growth rate ($r_2 > r_1$) (Figure 14). Again, there is a broad range of parameter values where the species coexist wedged between regions of competitive exclusion (Figure 14a). Figure 14b,c show the patch dynamics under successional-niche coexistence: both species have the same probability of colonizing a recently disturbed patch, but the faster growing species reaches its carrying capacity more quickly and

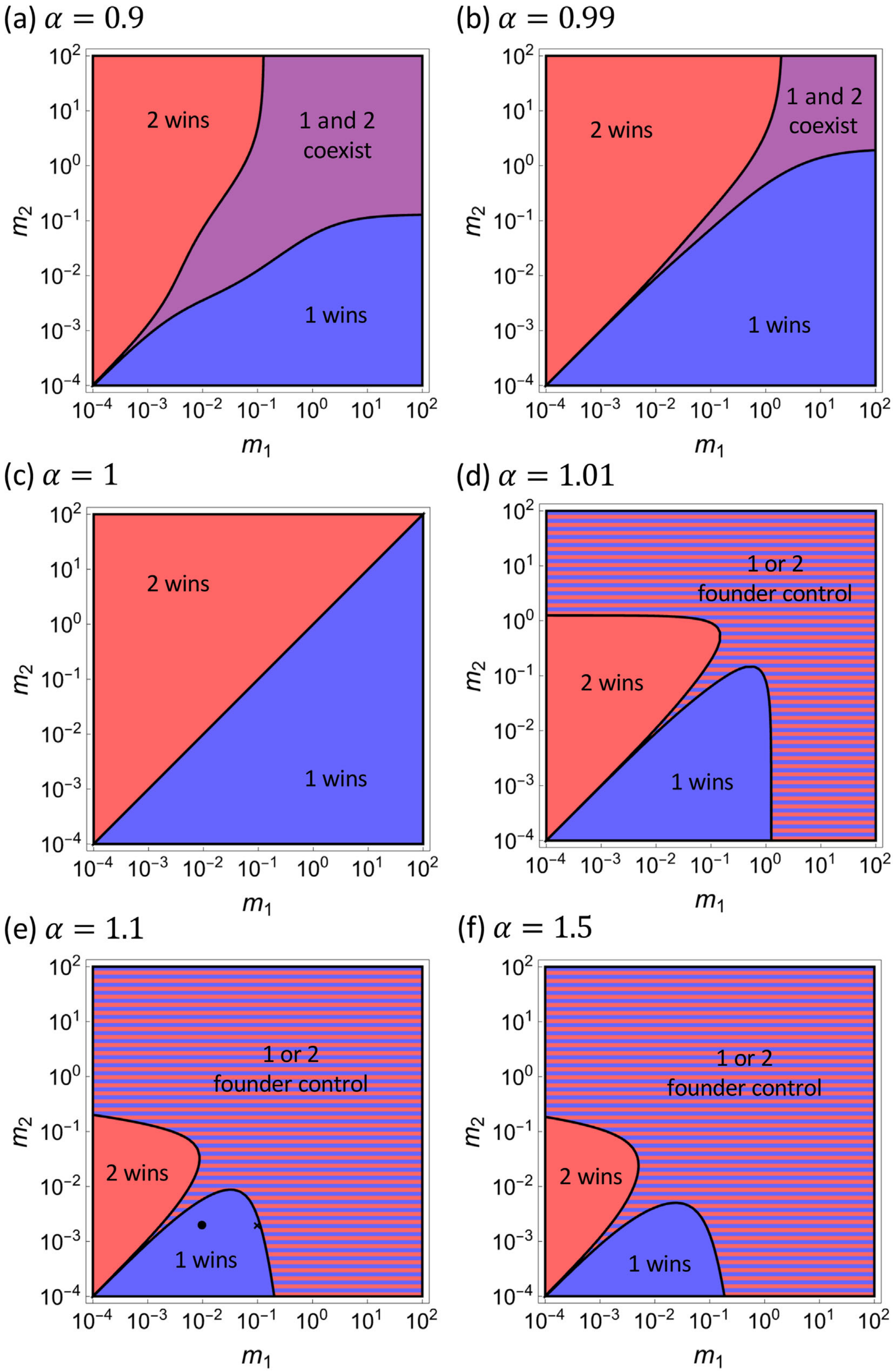

FIGURE 11 Outcomes in the metacommunity model for increasing symmetric ($\alpha_{12} = \alpha_{21} = \alpha$) interspecific competition coefficients: (a) $\alpha = 0.9$, (b) $\alpha = 0.99$, (c) $\alpha = 1$, (d) $\alpha = 1.01$, (e) $\alpha = 1.1$, (f) $\alpha = 1.5$. For parameters with classic LV coexistence or neutrality, the species with the higher dispersal rate performs better (panels a–c). However, with classic LV founder control, intermediate dispersal rates are optimal (panels d, e, f). Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = 50$, $X = 0$. Dot and X in panel (e) indicate parameter values simulated in Figure 12.

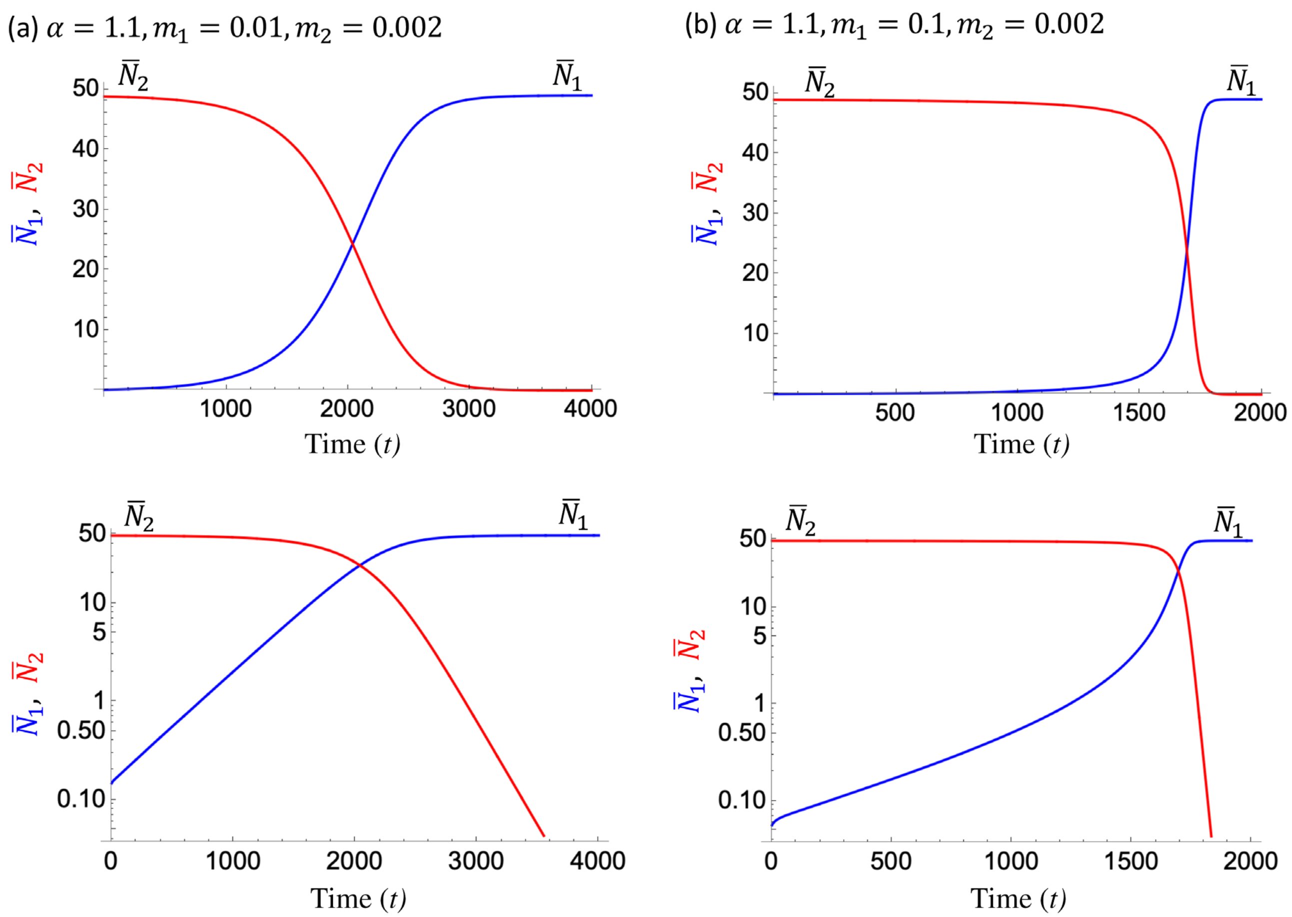

FIGURE 12 Invasion dynamics in the metacommunity model for two examples of regional competitive exclusion in the classic LV case of founder control: (a) $m_1 = 0.01$ (dot in Figure 11e), (b) $m_1 = 0.1$ (X in Figure 11e). Upper and lower panels are identical except for the scaling of the y-axis (arithmetic vs. logarithmic) to show faster-than-exponential growth in panel (b). Other parameters: $\alpha_{12} = \alpha_{21} = \alpha = 1.1$, $m_2 = 0.002$, $r_1 = r_2 = 1$, $K_1 = K_2 = 50$, $X = 0$.

then slows the takeover by the superior competitor (Figure 14c).

DISCUSSION

> "[P]erhaps *the* major weakness of traditional community ecology, and why it has so conspicuously failed to come up with many patterns, rules and workable contingent theory, is its overwhelming emphasis on localness."
>
> —Lawton, 1999

John Lawton's famous critique of community ecology levied harsh criticism of the field's focus on local dynamics. Metacommunity ecology provides one response that gives insight into the importance of regional dynamics on community outcomes (Leibold & Chase, 2017; Leibold et al., 2004). Yet, gaps in our understanding of the interplay between local and regional scales remain. In particular, although regional processes are no longer neglected, formal treatments considering both the local and regional scales have been rare (see Thompson et al., 2020). For example, regional processes are often treated in a patch dynamics framework, which ignores complexity within patches. Only by incorporating both local and regional processes can a complete picture of metacommunities emerge.

To address this gap, we built a series of simple models of two-species metacommunities based on Lotka–Volterra competition that includes dispersal, demographic stochasticity and random external disturbances. We studied these models in two settings, each appropriate for different natural systems. In the open-system models, we focused on one patch, with dispersal coming from a fixed regional community (island-mainland); in the closed-system, metacommunity model, we considered an infinite number of patches coupled by dispersal. The metacommunity model builds on the stochastic

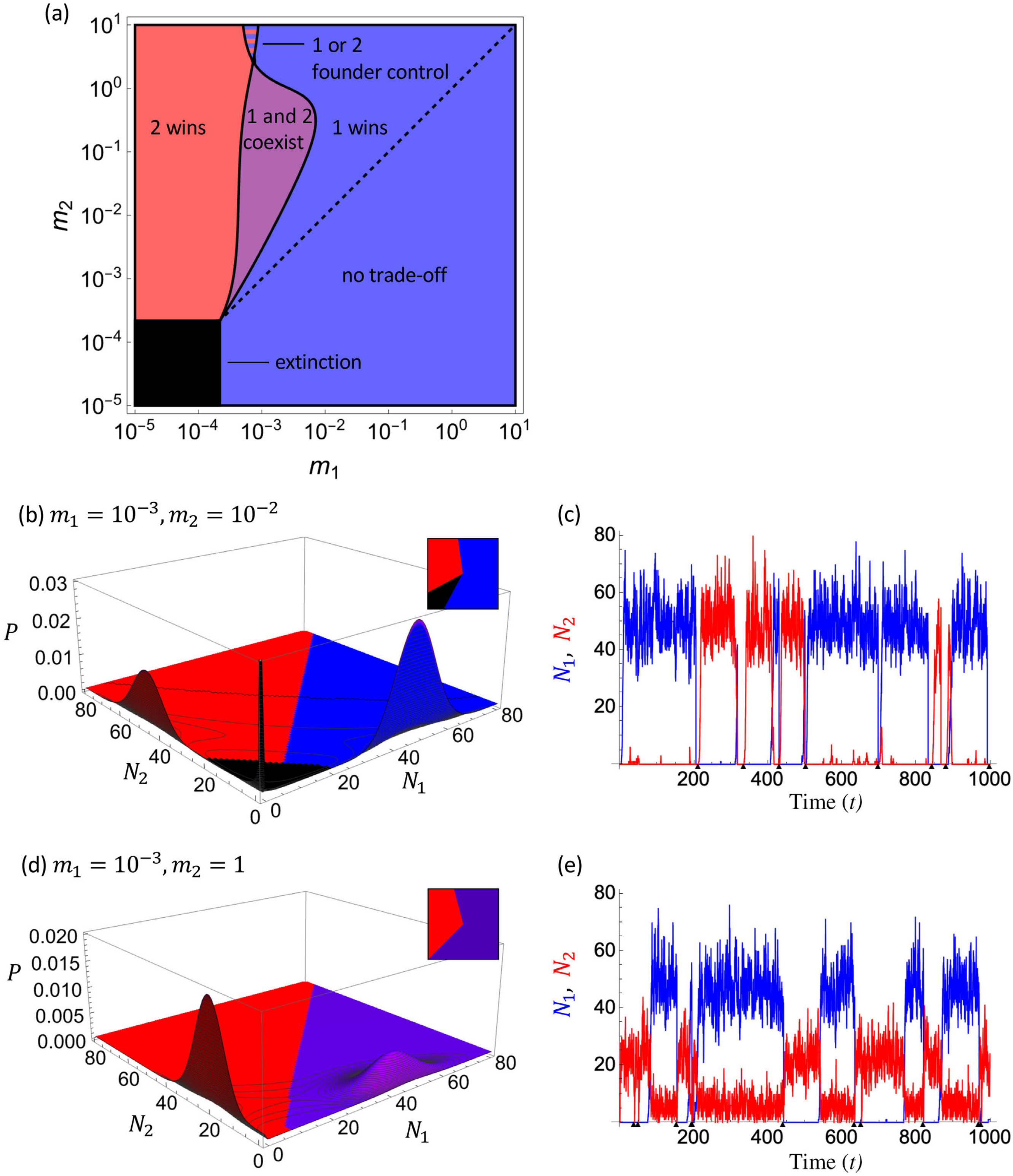

FIGURE 13 Competition-colonization trade-off in the metacommunity model can permit stable coexistence ($\alpha_{12} = 0.5, \alpha_{21} = 2$). (a) Overview of outcomes. (b, c) $m_2 = 10^{-2}$, (d, e) $m_2 = 1$. (b, d) Stationary probability distribution $\widehat{P}(N_1, N_2)$, colored according to coarse-grained states as in Figure 9. (c, e) Example time series. Disturbances are indicated by triangles under the x-axis. Other parameters: $r_1 = r_2 = 1$, $K_1 = K_2 = 50$, $m_1 = 10^{-3}$, $X = 0.01$.

open-system model by setting $N_R = \overline{N}$ so that the regional abundances emerge from the collection of local patches. The main difference is that the open-system models focus on a single patch embedded within a larger landscape. Species cannot be driven extinct due to continuous immigration, although patches can be dominated by one

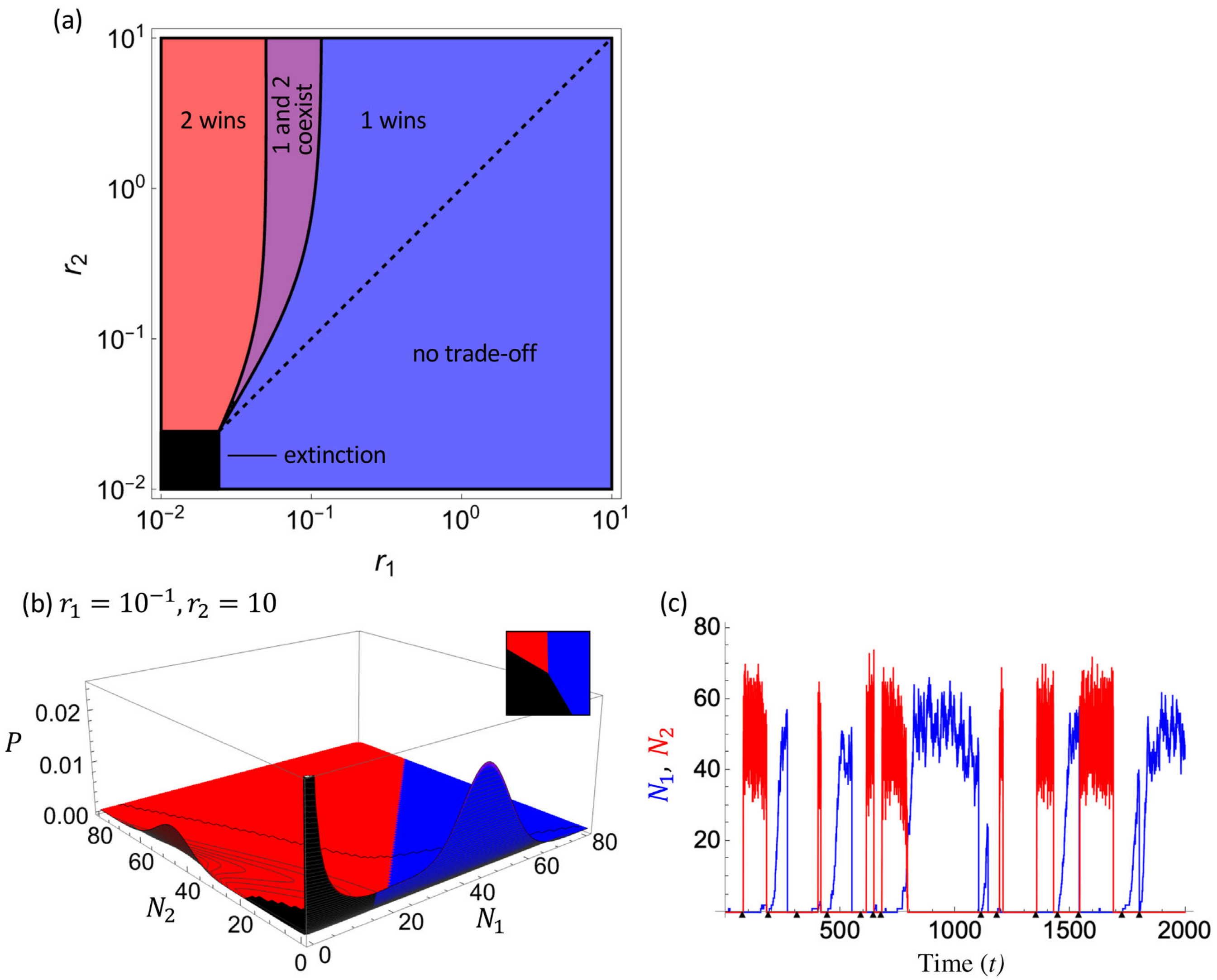

FIGURE 14 Successional-niche trade-off in the metacommunity model can permit stable coexistence ($\alpha_{12} = 0.5, \alpha_{21} = 2$). (a) Overview of outcomes. (b) Stationary probability distribution $\widehat{P}(N_1, N_2)$, colored according to coarse-grained states as in Figure 9. (c) Example time series. Disturbances are indicated by triangles under the x-axis. Other parameters: $r_1 = 10^{-1}, r_2 = 10$, $K_1 = K_2 = 50$, $m_1 = m_2 = 10^{-3}$, $X = 0.01$.

species. In contrast, the metacommunity model operates at a larger spatial scale, which allows distinct regional outcomes (competitive exclusion, coexistence, founder control) to emerge.

Scaling outcomes from local to regional

Because our metacommunity model includes both explicit stochastic within-patch population dynamics and the colonization and extinction of patches, it can be used to show the interplay between local and regional outcomes. Notably, outcomes from the classic LV model (Figure 1) do not necessarily scale up to the same regional outcomes. We summarize the major results below, contrasting the open- and closed-system models and connecting them with other models.

Classic LV coexistence

When the classic LV model predicts local coexistence ($\alpha_{12} < 1, \alpha_{21} < 1$), the metacommunity model often does as well (Figures 10 and 11a,b). However, the size of the coexistence region is reduced when dispersal is limited. If one species is a relatively poor competitor (α_{ij} close to one [Figure 10]) or a relatively poor disperser (small m_i [Figure 11a,b]) then it will be regionally excluded. Ecological drift makes coexistence more difficult, as also seen in the stochastic open-system model (Figures 7a,b and 9). Neuhauser and Pacala (1999) found a similar shrinking of the coexistence region in a spatially explicit stochastic model. In the presence of disturbances (Appendix S3: Figure S4), an additional impediment to coexistence arises. The decreased abundance N_i in jointly occupied patches reduces a species' effective colonization rate $m_i\overline{N}_i$, so it may be excluded if it was dispersal limited, as seen in a patch-occupancy model (fig. 3a in Klausmeier, 2001).

In the coexistence region, the probability distribution of community states $P(N_1, N_2)$ can be unimodal, bimodal, or even trimodal (Figures 7 and 9). Similar patterns of multimodality in stochastic models can result from what is known as a "saddle crawl-by" (Hastings et al., 2021), when an unstable equilibrium is attracting in one dimension (observed in a predator–prey model; Abbott & Nolting, 2017). A related phenomenon, "flickering," occurs when stochastic excursions to attractors become more common close to a critical transition (Scheffer et al., 2009), as observed in trophic cascades (Carpenter et al., 2008) and lake eutrophication (Carpenter & Brock, 2006). In our model, these effects result in increased time spent near the monoculture equilibria, especially for parameter values that are close to where the coexistence equilibrium loses its stability. However, multimodal probability distributions in our model can also occur for parameters that are firmly in the classic LV coexistence region (see also Capitán et al., 2015). Such multimodality requires stochasticity due to the discreteness of individuals and small population sizes. This phenomenon, known as discreteness-induced transitions, has previously been observed in chemical reaction networks (Bibbona et al., 2020; Togashi & Kaneko, 2001).

Classic LV exclusion

When the classic LV model predicts competitive exclusion $(\alpha_{ij} > 1, \alpha_{ji} < 1)$, the open-system models predict dominance by the superior competitor, with the inferior competitor persisting due to immigration from the region (Figures 2, 4, 6 and 9). This represents the mass-effects paradigm, which is a powerful explanation of local diversity (Koffel et al., 2022; Mouquet & Loreau, 2003).

The metacommunity model also predicts competitive exclusion in regions where the classic LV model predicts competitive exclusion if the competitors have equal growth and dispersal rates $(r_i = r_j, m_i = m_j)$ (Figure 10). However, in the face of external disturbances that reset patches $(X > 0)$, regional coexistence can occur through two well known mechanisms: the competition-colonization tradeoff between competitive ability and dispersal rate (Hastings, 1980; Hutchinson, 1951; Tilman, 1994; Figure 13) and the successional-niche trade-off between competitive ability and growth rate (Pacala & Rees, 1998; Figure 14). Our results echo classic patch-occupancy models of these trade-offs (Pacala & Rees, 1998; Tilman, 1994), although regional competitive exclusion of the superior local competitor is possible unlike in a strict hierarchical competition model (Tilman, 1994). Thompson et al. (2020) showed that alpha diversity increased with increased dispersal under a competition-colonization trade-off. We find the same in our model (Figure 13d,e) and dissect the mechanism underlying this phenomenon: the combination of patch dynamics and mass effects allows the superior colonizer to persist in patches dominated by the superior competitor. We also find new phenomena in the competition-colonization case, such as regional founder control (Figure 13a). In contrast with a patch-occupancy model (Orrock & Watling, 2010), we found that ecological drift does not preclude coexistence when coexistence is mediated by a competition-colonization trade-off. This discrepancy is likely due to the lack of explicit local dynamics in that model.

Classic LV founder control

The case when the classic LV model predicts founder control $(\alpha_{12} > 1, \alpha_{21} > 1)$ is the most complicated. For equal low dispersal rates $(m_1 = m_2)$, the stochastic open-system model shows dominance by one species, unless the competition coefficients are nearly balanced or the carrying capacities are very small, in which case the two alternative stable states led to a bimodal probability distribution (Figures 8a–d and 9b,c). In a single patch, this would represent stochastic switching between stable states (Figure 8b,d). In a landscape of patches subject to the same fixed immigration, this would appear as a spatial mosaic of the different states. Without stochastic switching, the founder-control region approaches the classic LV model for small dispersal rates (Figure 4c). Larger dispersal rates led to apparent coexistence, as immigration dominates local processes (Figures 4a, 8e,f and 9a).

The feedback between local and regional dynamics led to different results in the closed-metacommunity model (Figure 10). At high, equal dispersal rates, the regional outcome matches the classic LV outcome (Figure 10a). This is not surprising because the whole metacommunity is effectively well mixed and reflects the positive feedback where a regionally abundant species will send more immigrants to other patches, solidifying its hold on them. As dispersal becomes more limiting, the relative strength of the alternative stable states (i.e., the size of their basin of attraction and depth of their potential well; Nolting & Abbott, 2016) seen in the stochastic open system (Figure 9) can overcome this positive feedback, leading to competitive exclusion at the regional scale (Figure 10b–d). Ecological drift is essential to this result because it allows local patches to occasionally flip from one stable state to the other, more often from the weaker stable state to the stronger (see Appendix S2: Figure S1 for an example in the stochastic open-system model). This contrasts with the open-system results, whose spatial mosaic could be interpreted as long-term coexistence.

When dispersal rates are not equal, the regional outcome can be either competitive exclusion or founder control (Figure 11d–f). A species that disperses slightly more than its competitor can exclude it but, if it disperses too quickly, it spreads its individuals too thinly across the landscape, failing to hold onto patches and therefore making a successful invasion unlikely. The advantage of intermediate dispersal rates is reminiscent of the phalanx strategy of clonal plants (Lovett Doust, 1981). The positive feedback between regional abundance and local dynamics can be seen in the accelerating invasion rate as a species becomes established (Figure 12b).

Patch-occupancy models of local founder control predict either neutral regional dynamics (equal dispersal rates) or competitive exclusion by the better disperser (Klausmeier & Tilman, 2002; Shurin et al., 2004). The difference with the metacommunity model in this paper can be attributed to the lack of explicit local dynamics in these patch-occupancy models, which severs the feedback from regional abundance to local dynamics. Spatially explicit models with generic initial conditions also predict regional competitive exclusion (Neuhauser & Pacala, 1999), unless the habitat is discrete (Levin, 1974) or nonconvex (e.g., two spatial regions connected by a thin corridor; Mimura & Kawasaki, 1980), which can stabilize a spatial mosaic of the two species.

Classic LV neutrality

The case of identical competitors ($\alpha_{12} = \alpha_{21} = 1$) is mathematically degenerate, but serves as the basis of the neutral-theory paradigm (Hubbell, 2001). In our deterministic open-system model, this degenerate outcome is replaced by a unique stable equilibrium (Figure 4). In our stochastic open-system model, it results in a bimodal probability distribution at low dispersal (Figure 9b,c) and apparent coexistence at high dispersal (Figure 9a). Thus, when dispersal is incorporated, we find nothing exceptional about true neutrality: the outcome for slightly different competition coefficients is qualitatively similar.

In our closed-metacommunity model, local neutrality translates to regional neutrality only if species also have equal dispersal rates ($m_1 = m_2$), as evidenced by the intersection between outcomes precisely at $\alpha_{12} = \alpha_{21} = 1$ in Figure 10. However, the slightest difference in dispersal rates leads to competitive exclusion of the poorer disperser (Figure 11c). Once again, feedback between local and regional dynamics drives the difference between the stochastic open-system and metacommunity models.

Role of deterministic and stochastic processes

Our models include both deterministic and stochastic processes, and we present our results in terms of probability distributions of different community states. Here we highlight the role of deterministic and stochastic processes in determining the outcome of competition.

Deterministic processes

The metacommunity paradigms often focus on the situation of local competitive exclusion (Leibold & Chase, 2017). In contrast, our LV model continuously covers all local outcomes, from competitive exclusion to coexistence and founder control, with neutrality in the center (Figure 1; see also Thompson et al., 2020). The details of local selection have a strong impact on the regional outcome, although the borders between outcomes may shift (Figures 9 and 10).

Stochastic processes

Demographic stochasticity generally has the largest impact on small populations in simple birth–death models (Renshaw, 2011). This raises the question: what is small? Here, we see that coexistence is robust even in relatively small communities with a carrying capacity $K = 50$ individuals (Appendix S3: Figure S3) unless one species was nearly excluded in the deterministic model. Although this suggests that coexistence is robust to the effects of demographic stochasticity unless the community consists of only a handful of individuals, other results make clear that stochasticity can have a qualitative influence even in relatively large populations. For example, the outcome in the founder-control region remains different from the deterministic model even for $K = 200$.

The open-system models also show markedly different behavior in the founder-control region under low dispersal and increasing carrying capacities compared with their deterministic counterparts (compare Figure 4c and Appendix S3: Figure S1). In the limit of high carrying capacity K, the stochastic model should become more similar to the deterministic one due to relatively smaller fluctuations but, since it does not, it leaves us with the question of how to reconcile the two models on a biological level. As we show in Appendix S2, the answer is that while founder control is lost for the steady-state distribution in the stochastic model even under high carrying capacities, the time it takes for this to play out becomes increasingly long with increasing K. For even moderately large K, the time it takes for founder control to become lost is on the order of billions of generations. For all practical purposes then, the stochastic open system exhibits founder control for the time scales relevant to ecological communities. Thus, for large enough populations, the deterministic and stochastic open-system models can be said to agree on when there is founder control, provided we restrict the time available for the dynamics to unfold. This nuances our results on the loss of the founder-control region in the open-system models. Indeed, our results here suggest that founder control as a phenomenon cannot be properly gauged from the stationary distribution alone, and that an appropriate time scale must be set. Our model itself provides no easy way of determining this, and the appropriate time scale must ultimately be informed by the biology of the system of interest.

Furthermore, stochasticity is vital for a number of results from our metacommunity model, supporting the claim that its impact on community ecology is often qualitative and predictable as opposed to just "adding noise" to a deterministic trajectory (Shoemaker et al., 2020). Most importantly, stochasticity forces an exploration of phase space. As an example, classic LV bistability (i.e., local founder control) can result in complex and rich regional dynamics, since we see that switching between the two stable states will occur given a long enough waiting time.

Environmental stochasticity is also incorporated through random external disturbances that drive both species to become extinct locally. Coexistence through the competition-colonization and successional-niche trade-offs relies on these stochastic events, followed by faster population dynamics. This separation of regional and local timescales is an important aspect of understanding metacommunities.

Metacommunity paradigms

Even in a homogeneous environment, our models illustrate all of the metacommunity paradigms. The mass-effects paradigm is seen in the open-system models at high dispersal (Figures 2 and 8e), but is mostly missing from the metacommunity model except in the competition-colonization case at high dispersal (Figure 13d,e). This is not surprising since we assume a homogeneous environment, and mass effects require a stable source of immigrants that is lacking in the metacommunity model. Including underlying environmental variation would be necessary to see mass effects in our metacommunity model and represents an important future direction for unifying metacommunity ecology. In place of mass effects at high dispersal rates in the metacommunity model, species sorting occurs (Figure 10a). More generally, in our model, species sorting occurs whenever the regional outcome matches the expected local outcome, for example away from the boundaries between outcomes (open-system: Figure 9, metacommunity: Appendix S3: Figure S2). Patch dynamics occurs when there are multimodal probability distributions. This arises when there are external disturbances ($X > 0$), as in the competition-colonization (Figure 13) and the successional-niche cases (Figure 14). Patch dynamics can also result without disturbances at the border between outcomes due to ecological drift (Figure 9, Appendix S3: Figure S2).

Empirical tests

Although the main goal of this paper is to unify disparate strands of competition and metacommunity theory, our models (open-system and closed metacommunity) make testable predictions in the form of the bifurcation diagrams (Figures 9–11, 13, 14; Appendix S3: Figures S1–S4). They recapitulate the predictions of their constituent models (mass effects, the neutral theory, and patch dynamics, including competition-colonization and successional-niche trade-offs), so empirical tests of those models are also relevant to ours. However, our models also make some novel predictions: the intermediate optimum dispersal rate for invasion with local founder control (Figure 11d–f), the possibility of accelerating invasions (Figure 12b) and the regional exclusion of superior competitors in the competition-colonization scenario (Figure 13). One general recommendation for empiricists interested in testing this theory is to report the probability distribution of community states (as in Figures 6–8a,c,e), either over time or over space.

These predictions could be tested in laboratory microcosms using protists (e.g., Altermatt et al., 2015; Legault et al., 2019) or *Tribolium* beetles (e.g., Dallas et al., 2021; Mertz et al., 1976), in either a single patch subject to immigration (open-system) or an array of patches coupled by dispersal (metacommunity). In natural systems, experimental tests of the open-system model predictions may be more feasible, because single communities are the experimental units and regional abundances and dispersal rates could be manipulated.

The open-system model is more generally applicable, because it makes no assumptions about the regional setting, but since it assumes external immigration, it cannot address questions of true regional coexistence. The closed-metacommunity model could be tested using natural metacommunities, such as inquiline communities of pitcher plants (Miller & Kneitel, 2005) or nectar microbes (Chappell & Fukami, 2018).

Limitations and future directions

Although we believe our metacommunity model is useful due to both its simplicity and generality, it naturally has limitations. To maintain computational tractability, we make a number of simplifying assumptions. We assume an infinite number of patches in a spatially implicit framework allowing us to ignore correlations between regional events. In other words, an infinite number of patches guarantees that each patch is governed by the same master equation. Results from epidemiology (Ghoshal et al., 2004) and predator–prey dynamics (Sjödin et al., 2014) suggest that this is likely a useful approximation for much smaller and spatially explicit metacommunities. Based on their simulations, our model could reasonably be expected to capture the qualitative dynamics of metacommunities with only a handful of patches. That said, some qualitative differences would arise from including explicit space. Most notably, the homogenizing effect of dispersal on patches is weaker in spatially explicit models (Thompson et al., 2020). Relatedly, the cost of having too high a dispersal rate with local founder control (Figure 11d–f) is likely to have been weaker because species would not distribute themselves as thinly across the entire landscape (i.e., they could still amass at high densities in neighboring patches). Finally, exponential and accelerating invasion rates (Figure 12) may be replaced by traveling waves where invader abundance increases quadratically, unless dispersal kernels are fat-tailed (Kot et al., 1996).

Further, most of our results focus on long-term dynamics (except Figure 12), with the time scale to reach these dynamics often unclear, as we saw when comparing the stochastic and deterministic open-system models in the founder-control region. Such assumptions are necessary, however, as our model is computationally expensive. Consequently, we limit our analyses to communities with two species. Although our modeling framework expands naturally to an arbitrary number of species, it is unclear how to analyze our model practically if it were to be expanded to include more species (see also Capitán et al., 2017). This framework also lends itself to extensions that consider evolution in spatially structured populations (e.g., Leibold et al., 2019). In addition, we call on further work to analyze our current framework and apply it to a range of scenarios, such as different birth–death processes and community interactions beyond competition (e.g., predator–prey interactions; Sjödin et al., 2014).

Most significantly, we study a homogeneous underlying environment. This feature is particularly important, since environmental heterogeneity is central to the Leibold et al. (2004) classification of metacommunities into paradigms, species sorting and mass effects in particular. Including underlying patch heterogeneity is an important next step toward a general theory of competitive metacommunities that can fully capture all existing paradigms. Recent papers have developed such simulation models and analyzed them for multispecies communities (Ovaskainen et al., 2019; Shoemaker & Melbourne, 2016; Thompson et al., 2020). Due to the differing goals of these studies, the effects of dispersal and stochasticity on two-species competition were not analyzed thoroughly, as we have done here. Thus, extending our framework to consider a heterogeneous environment would serve as a valuable bridge between our model and other recent studies.

Conclusions

Most broadly, we provide perhaps the simplest possible model unifying the fundamental processes of community ecology of selection, drift, and dispersal. Doing so gives us a computationally tractable model of metacommunity ecology that moves beyond the standard paradigms. We highlight the flexibility of our approach through case studies like competition-colonization and successional-niche trade-offs. Finally, we show how the dynamical interplay of processes occurs at local and regional scales and ultimately leads to competitive outcomes in metacommunities.

AUTHOR CONTRIBUTIONS

Brian A. Lerch, Akshata Rudrapatna, Thomas Koffel, and Christopher A. Klausmeier developed and analyzed the stochastic open-system and metacommunity models. Nasser Rabi and Jonas Wickman analyzed the deterministic open-system model. Brian A. Lerch wrote the first draft of the manuscript, Christopher A. Klausmeier revised it, and all authors contributed to further revisions. Christopher A. Klausmeier obtained funding.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were used. Novel code (Mathematica and Fortran 77) used in this manuscript is available in Zenodo (Lerch et al., 2023; https://doi.org/10.5281/zenodo.8175016).

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