A unification of niche and neutral theories quantifies the impact of competition on extinction

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Abstract

Efforts to reconcile Hubbell’s neutral theory with classical niche theory have been limited by the lack of a nested analytical framework in which departures from the neutral hypothesis might be quantified in fits to empirical data. Here, we present the first extension of Hubbell’s theory to allow for asymmetries in competitive, density-dependent interactions such that niche dynamics stabilize or destabilize coexistence over intermediate time scales, while speciation and extinction regulate an unstable coexistence over evolutionary time scales. As a result, we obtain the first mechanistic metacommunity model to quantify the impact of competition on extinction. Intraspecific exceeding interspecific competition delays extinction beyond neutral expectations, while the opposing scenario generates a stochastic Allee effect that speeds extinction below a critical threshold in population abundance. Surprisingly, this unification of niche and neutral theory provides an economical resolution to the problem of short species lifetimes in Hubbell’s original model.

Keywords: niche theory, neutral theory, metacommunity, competition, extinction, Allee effect, biodiversity, coexistence, stochastic, master equation

Introduction

Classical niche theory and Hubbell’s neutral theory (Hubbell, 2001) offer two distinct mechanisms for the long-term maintenance of biodiversity in competitive communities. In niche theory, if species limit themselves more than each other, then asymmetric, density-dependent interactions stabilize coexistence, and species composition remains

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invariant over long time scales (Chesson, 2000). In neutral theory, functionally equivalent species drift steadily to extinction, but speciation balances extinction to maintain an unstable coexistence (Caswell, 1976; Hubbell, 2001; Chave, 2004). Here, we present the first analytical extension of Hubbell’s theory in which a niche mechanism stabilizes coexistence over intermediate time scales, while a balance of speciation and extinction regulates an unstable coexistence over evolutionary time scales. Previous efforts to reconcile niche and neutral theory, as reviewed below, only allow for density-independent asymmetries in ecological fitness and fail to provide a mechanism of niche stabilization. The nested structure of our unified framework, in which Hubbell’s model is recovered as the symmetric limit, may provide a powerful parameteric model for resolving the relative importance of niche versus neutral mechanisms in fits to empirical data. Our analytical results have distinct advantages over simulation-based work with regard to ease of interpretation and generalization. In particular, we demonstrate that models with zero-sum dynamics can be relaxed to allow for empty space, and ordinary dynamics are recovered in the appropriate limit. Furthermore, the mean dynamics of our stochastic theory yield Levins-type niche models that might be sufficient, over intermediate time scales, to gauge the relative strength of niche versus neutral dynamics based on time series data.

Integrating classical niche theory with the stochasticity of Hubbell’s neutral theory generates the first mechanistic metacommunity model to quantify the impacts of competition on extinction. Starting with the calculations of Leigh (1981) and Lande (1993), analytical studies of extinction, including population viability analysis (Morris & Doak, 2003), have focused on single-species models without explicit consideration of dynamical interactions with the surrounding community (Fagan & Holmes, 2006; Ovaskainen & Meerson, 2010). Recent progress in the physics literature has led to analytical calculations of extinction dynamics in two-species systems, including the Susceptibles-Infectives-Susceptibles model of epidemiology (Dykman et al., 2008) and the neutrally stable Lotka-Volterra equations (Parker & Kamenev, 2009). In this paper, we concentrate on analytical calculations of extinction dynamics in two-species competitive communities, but our analytical framework for niche-structured stochastic dynamics applies to communities with any number of species. The importance of niche stabilizing mechanisms in postponing extinction has been demonstrated empirically (Adler et al., 2010), and in our unified framework, when intraspecific exceeds interspecific competition, metastable states prolong species lifetimes beyond neutral expectations. Niche stabilization of Hubbell’s metacommunity offers a remarkably economical resolution to the problem of short species lifetimes in Hubbell’s original theory (Rosindell et al., 2010) and may restore point-speciation as a viable phenomenological model.
The development and testing of Hubbell’s theory

In an attempt to model species-rich tropical forests where gaps are rapidly filled by new growth, Hubbell (2001) abandoned niche theory for a neutral model of zero-sum dynamics where migration couples a dispersal-limited, or local, community to the neutral speciation and extinction dynamics of a regional metacommunity. A relatively small number of individuals in the local community allows for rapid equilibration to metacommunity fluctuations. This separation of temporal and spatial scales is sufficient to generate the commonly observed mode in Relative Species Abundance (RSA) distributions that eluded the pioneering work on neutral models by Caswell (1976). As a result, Hubbell’s mechanistic framework is arguably the first to prescribe interactions at the level of individuals and then predict realistic patterns of large-scale diversity.

Although Hubbell’s metacommunity has inspired some striking fits to data (see, e.g., Muneepeerakul et al. (2008)), the point speciation mode of Hubbell’s metacommunity model predicts high incidence of rare species and short average lifetimes of only a few generations (Ricklefs, 2003; Nee, 2005; Ricklefs, 2006). Hubbell considered the alternative of random fission as a model of allopatric speciation (Hubbell, 2001), and a recent analysis by Etienne & Haegeman (2010) found that this approach yields improved predictions for species rarity and longevity. Proposals have appeared for additional mechanisms, including peripheral isolate speciation (Hubbell, 2003) and density-independent speciation (Etienne et al., 2007b; Haegeman & Etienne, 2009), among others (Hubbell & Lake, 2002; Allen & Savage, 2007). However, none of them outperformed point speciation in fits to RSA data (Etienne et al., 2007b) until the recent innovation of protracted speciation by Rosindell et al. (2010), in which marginal improvements to RSA fits were accompanied by more realistic estimates of lifetimes and speciation rates.

Despite concerns over the phenomenology of Hubbell’s metacommunity, much of the neutral theory literature focuses on local community dynamics. In simulations where the only two free parameters are speciation and migration levels, Hubbell (2001) found remarkably good fits to data from various closed-canopy tree communities, the mixed mesophytic forest on the Cumberland Plateau of Kentucky, a planktonic copepod community of the northeastern Pacific gyre, and the bat community of Barro Colorado Island, Panama, among others. However, in fits to data from forest plots along the Manu River of Amazonian Peru, abundances for the top seven species exceeded the neutral prediction. Hubbell (2001) referred to these discrepancies as “ecological dominance deviations” and, in an extension of his simulation, found that small asymmetries in survival across species were sufficient to obtain a good fit. These considerations anticipated future calls for an analytical expansion of neutral theory to allow for niche stabilizing asymmetries (see, e.g., Alonso et al. (2006)).

The publication of Hubbell’s book initially triggered a heated debate over the rel-
ative merits of neutral theory in fits to RSA data. Volkov et al. (2003) derived an analytical prediction for the RSA distribution of Hubbell’s local community at equilibrium, and a fit to the well-known tree data set taken from a 50-ha plot on Barro Colorado Island outperformed the classical lognormal distribution. But McGill (2003) soon countered with a simulation-based fit that came to the opposite conclusion. A later study by Volkov et al. (2005) generalized Hubbell’s theory of local communities to allow for symmetric density-dependence that favors rare species. This alternative formulation matched Hubbell’s original model in fits to data on six tropical forests, but Chave et al. (2006) replied with an analysis that favored Hubbell’s model in all six cases. Meanwhile, Etienne (2005) calculated a sampling formula for Hubbell’s local community. When compared against a niche-motivated multivariate Poisson lognormal distribution in a Bayesian analysis, the neutral sampling formula provided a superior fit to data on a tropical freshwater fish community but not data from a neotropical tree community (Etienne & Olff, 2005).

Progress so far on reconciling niche and neutral theory

A growing body of evidence suggests that niche and neutral processes may both generate unimodal RSA distributions. Indeed, niche dynamics, neutral dynamics, and two other coexistence mechanisms yielded strikingly similar predictions for overall patterns of diversity in spatially explicit, individual-based simulations (Chave et al., 2002). Numerical work by Purves & Pacala (2005) confirming that “neutral pattern does not imply neutral process” were followed by the analytical work of Chisholm & Pacala (2010) demonstrating asymptotic equivalence of niche and neutral predictions for RSA distributions in high-diversity ecological communities. Further confirmation arises from Noble et al. (2011) who derived an asymmetric extension of Hubbell’s theory and demonstrated that strong mass-effects may swamp differences in ecological fitness to generate RSA distributions consistent with the neutral prediction. On the empirical side, RSA fits were a poor diagnostic of neutrality in data from a Mexican tropical forest (Kelly et al., 2008).

In light of a growing body of evidence, Adler et al. (2007) stated emphatically that the niche versus neutral debate cannot be resolved by analyzing species abundance patterns and that attention should focus instead on measuring both the strength of niche stabilization mechanisms and the size of fitness differences. The subsequent study by Adler et al. (2010) found strong niche stabilizing mechanisms in a sagebrush steppe community despite small fitness differences among species. Related work by Levine & HilleRisLambers (2009) concluded that niche differences stabilize dynamics in communities of serpentine annual plants. Meanwhile, Volkov et al. (2009) deduced the
effective pairwise interaction strengths among the twenty most abundant species in the well-known 50-ha plot on Barro Colorado Island and reported that interspecific interactions are weak in comparison to intraspecific interactions – the result expected from a neutral community of noninteracting species. More recently, the analysis by Stokes & Archer (2010) of shrub assemblages in a parkland savanna found that the best models accommodated both niche and neutral processes.

The above results suggest that “the niche and the neutral models are in reality two ends of a continuum with the truth most likely in the middle” (Chase & Leibold, 2003, p. 179). In an early effort to examine that continuum, Tilman (2004) studied community assembly under a combination of competitive tradeoff theory and neutral demographic stochasticity. Later, Gravel et al. (2006) developed a spatially explicit simulation of local communities in which niche and neutral mechanisms span a continuum of dynamics ranging from competitive to stochastic exclusion. Significant analytical progress was marked by the work of Kadmon & Allouche (2007) that forged a unified stochastic framework for niche theory and the island biogeography of MacArthur & Wilson (1967) which inspired much of Hubbell’s work. Analytical efforts to break neutrality in the local community began with a demonstration by Etienne et al. (2007a) that the equilibrium sampling formula is identical for an ordinary, nonzero-sum community of independent species. Haegeman & Etienne (2008) expanded on this idea to allow for community-level density-dependence in local community dynamics, and Allouche & Kadmon (2009) soon established a general framework for calculating the equilibrium RSA distributions of both neutral local communities and their non-neutral extensions that allows for asymmetries in birth, mortality, and immigration rates. Related analytical work by Noble et al. (2011) retained the explicit assumption of zero-sum dynamics and provided the first asymmetric formulation of metacommunity and local community dynamics to yield Hubbell’s theory in the symmetric limit.

Despite these advances, incorporating niche mechanisms of stabilization into neutral theory requires further work to allow for asymmetric density-dependence. Although the state-space model of Mutshinda & O’Hara (2011) may prove valuable in discriminating between niche interactions and demographic stochasticity, Haegeman & Loreau (2011) have made the greatest progress to date in reconciling niche and neutral dynamics. In adding demographic stochasticity and immigration to a classical Lotka-Volterra model, they generated an analytical theory of local communities that combines niche and neutral dynamics. However, the zero-sum rule is absent from the model of Haegeman & Loreau (2011), so Hubbell’s theory cannot be recovered in the symmetric limit. More importantly, the question remains of how to incorporate niche dynamics into Hubbell’s metacommunity such that mechanisms of stable and unstable coexistence operate in tandem. Here, we construct non-neutral extensions for the metacommunity and the lo-
cal community that allow for niche stabilization over intermediate time scales, balance speciation and extinction dynamics over long time scales, yield Hubbell’s model as the symmetric limit, and quantify the impact of competition on extinction.

**Preliminaries**

To provide an explicit point of comparison in the sections to follow, we define the classical niche model to be a system of ordinary differential equations where

\[
\frac{dn_i}{dt} = n_i \left( r_i - \sum_{j=1}^{S} a_{ij} n_j \right),
\]

for each of the species, labelled 1 thru \( S \). The \( n_i \) are abundances; the \( r_i \) are intrinsic growth rates; and the \( a_{ij} \) are per capita interaction strengths. This article will focus on the community dynamics of ecologically similar species where all interactions are competitive, i.e. \( a_{ij} > 0 \) for all \( i \) and \( j \). The standard requirements for niche stabilized coexistence emerge from the simplest classical model. Consider a two-species community where intraspecific interactions are positive, i.e. \( a_{11}, a_{22} > 0 \). The coexisting fixed point

\[
\begin{align*}
n_1^* &= \frac{a_{22}r_1 - a_{12}r_2}{a_{11}a_{22} - a_{12}a_{21}}, \\
n_2^* &= \frac{a_{11}r_2 - a_{21}r_1}{a_{11}a_{22} - a_{12}a_{21}},
\end{align*}
\]

is stable if

\[
\begin{align*}
\frac{a_{21}}{a_{11}} &< r_2, \\
\frac{a_{12}}{a_{22}} &< r_1.
\end{align*}
\]

This form of the stability criteria, expressed in terms of intrinsic growth rates rather than carrying capacities, was highlighted by Vandermeer (1975), and we will refer to Eq. 3 as the “competitive stability criteria”. If all species are ecologically equivalent, such that \( r_i = r \) and \( a_{ij} = a \) for all \( i \) and \( j \), the inequalities are violated and coexistence is destabilized. This phenomenology reflects Gause’s axiom that species must exhibit some degree of differentiation in order to stably coexist (Chase & Leibold, 2003). Furthermore, the competitive stability criteria imply that \( a_{12}a_{21} < a_{11}a_{22} \), so the geometric mean of intraspecific competition must exceed the geometric mean of interspecific competition. This requirement for niche stabilization, that species limit themselves more than other species, was emphasized by Chesson (2000) in a closely related model.
The classical niche model provides important insights on the relationship between competition and stable coexistence but fails to quantify the fluctuations that may lead to extinction. Deterministic models, such as Eq. 1, approximate the mean dynamics of large, stable populations where probabilities of extinction can be ignored on sufficiently short time scales. Smaller populations require a more mechanistic approach to capture the discrete nature of birth and death events and the uncertainty surrounding the timing of those events. In this context, exact population densities at future times cannot be predicted with certainty based on currently available information. To be specific, given a discrete vector of known initial community abundances, $\vec{N}(t = 0) = (N_1(t = 0), \ldots, N_S(t = 0))$, we cannot predict an exact value for future abundances, $\vec{N}(t)$. Instead, we aim to predict the probability, $P_{\vec{n}}(t)$, of finding the community in state $\vec{n} = (n_1, \ldots, n_S)$ at time $t$. $\vec{N}(t)$ is called a stochastic process and each reasonable $\vec{n}$ is referred to as an accessible state. The time-dependent probability of each accessible state, $P_{\vec{n}}(t)$, is treated as a dynamical variable that increases or decreases based on transition rates to and from other states

$$\frac{dP_{\vec{n}}}{dt} = \sum_{\text{all other states}} \text{(Rate of transition to } \vec{n} \text{ from other state)} \times P_{\text{other state}} - \sum_{\text{all other states}} \text{(Rate of transition to other state from } \vec{n}) \times P_{\vec{n}} \quad (4)$$

This equation of motion for $P_{\vec{n}}(t)$, called a “master equation”, provides a powerful platform for mechanistic modeling in ecology (Nisbet & Gurney, 2003). In particular, a master equation framework not only captures extinction dynamics due to demographic fluctuations in small populations but also yields a prescription for the mean dynamics of large populations where fluctuations are small. Neutral theories that maintain diversity through a balance of speciation and extinction, such as Hubbell’s theory, are typically formulated as master equations.

In the sections to follow, we demonstrate that niche stabilization can be added to neutral theories by expanding the master equations to allow for a density-dependent per capita rate of successful reproduction

$$w_{i\vec{n}} \equiv w_{i0} \exp \left( -\sum_{j=1}^{S} a_{ij} n_j / w_{i0} \right), \quad (5)$$

which we refer to simply as the ecological fitness of species $i$. On an intuitive level, this parameterization may be the simplest way to allow species to limit themselves and each other while guaranteeing that ecological fitnesses are always positive, an important requirement for the master equations to follow. On a more formal level, we might
consider \( w_{i\vec{n}} \) to be an intrinsic ecological fitness, \( w_{i0} \), multiplied by the Poisson probabilities, \( \exp(-a_{ij}n_j/w_{i0}) \), that no deaths occur due to interactions with species \( j \). But regardless of its origin, we will demonstrate that the chosen form of density-dependent ecological fitness is remarkably useful in creating a non-neutral framework that combines niche stabilization and demographic stochasticity in a single theory. Niche mechanisms allow for metastabilities that stabilize populations on intermediate time scales, while large fluctuations allow for a balance of extinction and speciation over long time scales. In the first two sections we demonstrate how density-dependent ecological fitness can stabilize the simplest models of ordinary and zero-sum stochastic dynamics. We then expand on the zero-sum model to generate a niche-stabilized extension of Hubbell’s metacommunity and local community models. For each model, we quantify the impact of competitive niche dynamics on mean times to extinction in metacommunities and mean times to extirpation in local communities, where immigration allows populations to recover.

**Niche stabilization of a simple birth-death process**

The ordinary dynamics of a multivariate birth-death process are governed by the master equation

\[
\frac{dP_{\vec{n}}}{dt} = \sum_{i=1}^{s} \left( g_{i\vec{n}-\vec{e}_i} P_{\vec{n}-\vec{e}_i} \Theta(n_i - 1) + r_{i\vec{n}+\vec{e}_i} P_{\vec{n}+\vec{e}_i} - g_{i\vec{n}} P_{\vec{n}} - r_{i\vec{n}} P_{\vec{n}} \Theta(n_i - 1) \right),
\]

where \( r_{i\vec{n}} \) is the density-dependent rate of removal for an individual of species \( i \), \( g_{i\vec{n}} \) is the rate of gain, \( n_i \geq 0 \), and the step-function \( \Theta(x) \) is 0 for \( x < 0 \) and 1 otherwise. We assume a density-dependent per capita growth rate, \( w_{i\vec{n}} \), but a density-independent per capita death rate, \( d_i \), such that

\[
g_{i\vec{n}} \equiv \lim_{\Delta t \to 0} \frac{P(\vec{N}(t + \Delta t) = \vec{n} + \vec{e}_i | \vec{N} = \vec{n})}{\Delta t} = w_{i\vec{n}} n_i,
\]

\[
r_{i\vec{n}} \equiv \lim_{\Delta t \to 0} \frac{P(\vec{N}(t + \Delta t) = \vec{n} - \vec{e}_i | \vec{N} = \vec{n})}{\Delta t} = d_i n_i.
\]

This is a simple birth-death process of neutral drift if \( w_{i0} = b \), \( a_{ij} = 0 \), and \( d_i = d \) for all \( i \) and \( j \), such that ecological fitness is density-independent and all species are equivalent. We now argue that density-dependent ecological fitnesses allow for metastabilities that promote coexistence on intermediate time scales and delay extinction.
The mean dynamics of Eq. 6 are given by a system of ordinary differential equations where for each species $i$ (see SI.1)

$$\frac{dn_i}{dt} = n_i(w_{ini} - d_i),$$

(8)

and, in this context, $n_i = n_i(t)$ is a continuous variable. Although limit cycles may arise in two-species predator-prey systems, as discussed in Box 1, our focus remains on the dynamics of competitive communities, and the prescription in Eq. 8 reduces to more familiar models in various limits. For a single species system, a transformation to discrete time yields the Ricker model (see SI.2), so for two or more species, we have a generalization of the Ricker model to continuous-time community dynamics. We also recover the classical niche model upon taking a first-order expansion of the exponential that appears in $w_{ini}$ and identifying the $w_{i0} - d_i$ with the $r_i$ in Eq. 1. This approximation is valid where $\sum_{j=1}^{S} a_{ij}n_j << 1$ for every $i$.

But even without approximation, the phenomenology arising from Eq. 8 is strikingly similar to results from the classical niche model. In a two-species community where $a_{11}, a_{22} > 0$, the fixed-point abundances

$$n_1^* = \frac{a_{22}w_{10}\log(w_{10}/d_1) - a_{12}w_{20}\log(w_{20}/d_2)}{a_{11}a_{22} - a_{12}a_{21}},$$

$$n_2^* = \frac{a_{11}w_{20}\log(w_{20}/d_2) - a_{21}w_{10}\log(w_{10}/d_1)}{a_{11}a_{22} - a_{12}a_{21}},$$

(9)

where “log” denotes the natural logarithm, are positive and stable for

$$w_{20}\log(w_{20}/d_2)\frac{a_{12}}{a_{22}} < w_{10}\log(w_{10}/d_1),$$

$$w_{10}\log(w_{10}/d_1)\frac{a_{21}}{a_{11}} < w_{20}\log(w_{20}/d_2).$$

(10)

These criteria are identical to the competitive stability criteria if we identify $w_{10}\log(w_{10}/d_1)$ and $w_{20}\log(w_{20}/d_2)$ with $r_1$ and $r_2$, respectively. In particular, stable coexistence hinges on familiar niche mechanisms: species must be asymmetric such that the geometric mean of intraspecific competition exceeds the geometric mean of interspecific competition. A niche stablized fixed-point in the mean dynamics of Eq. 8 corresponds to a metastability in the stochastic process governed by Eq. 6 that promotes coexistence on intermediate time scales (Van Kampen 2001, Ch. 8). Although the mean dynamics fail to capture large fluctuations in the stochastic model that drive populations to extinction, the existence of a metastability postpones extinction.
Niche stabilization of a simple Moran model

We now consider zero-sum dynamics in a community of \(J\) individuals where the accessible states, \(\vec{n} = (n_1, \ldots, n_S)\), must satisfy \(0 \leq n_i \leq J\) for each \(i\) and \(\sum_{i=1}^{S} n_i = J\). The stochastic process follows a simple multivariate Moran model (see Ewens (2004)), where the master equation can be written as

\[
\frac{dP_{\vec{n}}}{d\tau} = \sum_{i=1}^{S} \sum_{j=1, j \neq i}^{S} (T_{ij\vec{n}+\vec{e}_i-\vec{e}_j}P_{\vec{n}+\vec{e}_i-\vec{e}_j} - T_{ji\vec{n}}P_{\vec{n}}) \Theta_{ij\vec{n}},
\]

(11)

with \(\Theta_{ij\vec{n}} \equiv \Theta(J - (n_i + 1))\Theta(n_j - 1)\) and a dimensionless measure of time, \(\tau\). A common death rate sets the overall timescale in the zero-sum transitions given by

\[
T_{ij\vec{n}} \equiv \lim_{\Delta\tau \to 0} \frac{P\left(\vec{N}(\tau + \Delta\tau) = \vec{n} - \vec{e}_i + \vec{e}_j | \vec{N} = \vec{n}\right)}{\Delta\tau} = \frac{n_i}{J} \left(\sum_{k=1}^{S} \frac{w_{i\vec{n}-\vec{e}_i}n_j}{w_{k\vec{n}-\vec{e}_i}n_k - w_{i\vec{n}-\vec{e}_i}}\right).
\]

(12)

The probability of species \(i\) being selected for death is just the relative abundance, \(n_i/J\), of species \(i\). The probability that species \(j\) recruits and establishes in the vacancy left by species \(i\) is determined by drawing from the available pool of offspring in which the representation of species \(k\) is determined by \(w_{k\vec{n}}n_k\). Various subtractions in the expression for \(T_{ij\vec{n}}\) account for the death in species \(i\) that precedes the reproduction, recruitment, and establishment of species \(j\). Eq. (11) with Eq. (12) reduces to a simple model of zero-sum neutral drift in a symmetric community where \(w_{i0} = b\) and \(a_{ij} = a_j\) for all \(i\) and \(j\). The former condition ensures that intrinsic fitnesses are equivalent, while the latter ensures the absence of a niche stabilizing mechanism; together, these conditions are the requirements for neutrality highlighted by Adler et al. (2007). Breaking these symmetries allows for metastabilities that promote coexistence on intermediate time scales and delay extinction.

The mean dynamics of Eq. (11) can be written as a Levins model (Levins & Culver, 1971), and for sufficiently weak competitive asymmetries such that \(w_{i\vec{n}} << \sum_{k=1}^{S} w_{k\vec{n}}n_k\) and \(a_{ij} << \sum_{k=1}^{S} a_{ik}n_k\) for every \(i\) and \(j\), we have (see SI.1)

\[
\frac{dp_i}{d\tau} = c_i(\vec{p})p_i(1 - p_i) - \sum_{j=1, j \neq i}^{S} c_j(\vec{p})p_ip_j,
\]

(13)
where $p_i \equiv n_i/J$ is a continuous variable. The colonization and competition terms share a common Beddington-DeAngelis coefficient [Beddington 1975, DeAngelis et al. 1975]

$$c_i(\vec{p}) = \frac{w_i(\vec{p})}{J \sum_{k=1}^{S} w_k(\vec{p}) p_k},$$

where each $w_i(\vec{p})$ is obtained from the expression for $w_{i\vec{n}}$ with the substitution of $p_i J$ for $n_i$. The mean dynamics of Eq. 13 prescribe zero-sum niche dynamics for a community with any given number of species and individuals (see SI.3). The phenomenology is remarkably similar to the classical niche model for a two-species system, and we will refer to Eq. 13 as a “Levins niche model”. Fixed-point relative abundances

$$p_1^* = \frac{B_2}{B_1 + B_2};$$
$$p_2^* = 1 - p_1^*,$$

where

$$B_1 = a_{11} J/w_{10} - a_{21} J/w_{20} - \log(w_{10}/w_{20}),$$
$$B_2 = a_{22} J/w_{20} - a_{12} J/w_{10} + \log(w_{10}/w_{20}),$$

are positive and stable for

$$w_{10} e^{a_{21} J/w_{20}} < w_{20},$$
$$w_{20} e^{a_{12} J/w_{10}} < w_{10},$$

which implies that $a_{12} a_{21} < a_{11} a_{22}$. As in the previous section, the correspondence to the competitive stability criteria and the familiar mechanisms of niche stabilization is clear.

If the first species competes with one or more symmetric species, the full multivariate stochastic dynamics of Eq. 11 can be reduced to a univariate master equation for the marginal dynamics of the first species (see SI.4). Fig. 1 plots the temporal evolution of the conditional abundance probability distribution, $P_{cn_{1,\tau}}$, as determined by Eq. SI.4.1 after excluding situations in which the first species reaches total extinction or complete dominance. Panels 1a, 1b, and 1c correspond, respectively, to scenarios of neutrality, interspecific exceeding intraspecific competition, and intraspecific exceeding interspecific competition. In all cases, the conditional probabilities approach a quasi-stationary distribution at long times. Compared to the neutral case, an excess of interspecific competition destabilizes the system by inducing a bimodal distribution where one of the
two species dominates over short time scales with a high probability. This bistability corresponds to an unstable fixed-point of the mean dynamics and signals a stochastic Allee effect where quasi-extinctions in the first species occur in transitions from the upper to the lower abundance mode. By contrast, an excess of intraspecific competition generates a single peak in the conditional distribution. This peak is a metastability that corresponds to a stable fixed-point of the mean dynamics. Although absorbing states in the simple Moran model guarantee monodominance by a single species at long times, a metastability for coexistence delays extinction on intermediate time scales.

Parallels between the phenomenology of niche stabilization for ordinary dynamics and zero-sum dynamics suggest the possibility of a formal connection between the two theories. In SI.5, we extend the multivariate Moran model and its mean dynamics to allow for empty space. Summations run to $S + 1$ and the stochastic variable $N_{S+1}(\tau)$ tracks the number of unoccupied patches. For large zero-sum communities where the vast majority of spaces are unoccupied, population dynamics are well-approximated, after a rescaling of time, by ordinary dynamics. Fig. 2 summarizes connections among the niche stabilized stochastic processes and mean dynamics of the first two sections. All models contain a neutral theory in the symmetric limit.

Of course, neither of the two stochastic frameworks discussed thus far offers a valid model of biodiversity over long time scales. In the simple birth-death process, each species will either become extinct or approach infinite abundance. In the simple Moran
Figure 2: A summary of connections among the niche-stabilized stochastic and mean dynamics as discussed in the first two sections of this paper. The remaining two sections analyze non-neutral metacommunity and local community models that add speciation and immigration, respectively, to the niche stabilized Moran model. All models contain a neutral theory in the symmetric limit.
model, a single species will dominate. The next two sections extend the Moran model of Eq. [11] by allowing speciation or migration to remove the absorbing states at monodominance that inhibit the long-term maintenance of species diversity. These non-neutral frameworks inherit the niche stabilization of our simple Moran model but yield Hubbell’s theory of metacommunities and local communities in the neutral limit.

Niche stabilization of Hubbell’s metacommunity

A previous extension of Hubbell’s metacommunity theory, with point-speciation, allowed for asymmetries in ecological fitness and speciation probability (see Box 2, Eq. [B2.1]). We now expand on that asymmetric framework by introducing density-dependence in ecological fitness. To do this, we replace all the density-independent \( w_i \) that appear in Eq. [B2.1] by the density-dependent \( w_i \vec{n} - \vec{e}_i \) to obtain a new master equation. The simple Moran model is recovered when all speciation probabilities vanish, and a multivariate formulation of Hubbell’s metacommunity theory is included as the symmetric limit. The mean dynamics approximating our non-neutral metacommunity dynamics can be written as a Levins model, and we once again assume weak competitive asymmetries to obtain

\[
\frac{dp_i}{d\tau} = s_i(\vec{p}) + c_i(\vec{p})p_i (1 - p_i) - e(\vec{p})p_i - \sum_{j=1, j \neq i}^S c_j(\vec{p})p_ip_j + O\left(\frac{1}{S}\right), \tag{18}
\]

where \( O(1/S) \) indicates additional terms that are negligible as the number of species becomes large and

\[
\begin{align*}
s_i(\vec{p}) &= \frac{\nu_i}{JM} \frac{w_i(\vec{p})}{\sum_{k=1}^S w_k(\vec{p})}, \\
c_i(\vec{p}) &= \frac{1 - \nu_i}{JM} \frac{w_i(\vec{p})}{\sum_{k=1}^S w_k(\vec{p})p_k}, \\
e(\vec{p}) &= \sum_{j=1}^S \frac{\nu_j}{JM} \frac{w_j(\vec{p})}{\sum_{k=1}^S w_k(\vec{p})}. \tag{19}
\end{align*}
\]

In addition to colonization and competition, we now find a source term, with coefficient \( s_i(\vec{p}) \), and an extinction term, with coefficient \( e(\vec{p}) \), arising from nonzero speciation probabilities. The mean dynamics of Eq. [18] approximate non-neutral metacommunity dynamics given any fixed number of species and individuals. In the neutral limit, we find

\[
\frac{dp_i}{d\tau} = \nu \left(\frac{1}{S} - p_i\right), \tag{20}
\]
such that all species completely decouple and drift toward extinction at a common rate as $S$ becomes large. For a nearly neutral metacommunity with low levels of speciation, a fixed-point analysis of Eq. 18 yields small corrections to the stability criteria of the simple Moran model (see SI.6), so we expect that our non-neutral metacommunity model inherits a niche stabilization mechanism.

Confirmation is provided by a calculation of extinction times for the asymmetric species in a nearly neutral metacommunity (see SI.7). Fig. 3a plots $\tau_E$ against $p_{10} \equiv n_{10}/J_M$, while Fig. 3b plots the corresponding flows, $dp_1/d\tau$ versus $p_1$, of the mean dynamics. In the fully neutral limit, demographic stochasticity drives all species toward extinction in the absence of a stabilizing mechanism (Chesson, 2000; Hubbell, 2001), and the mean dynamics yield a single stable fixed point at $p_1 = 0$. For the case where interspecific exceeds intraspecific competition, $\tau_E$ falls below (above) neutral expectations when $p_{10}$ is low (high). The existence of an inflection point in the $\tau_E$ versus $p_{10}$ curve signals a stochastic Allee effect, as discussed by Dennis (1989, 2002) and Allen et al. (2005). Indeed, the mean dynamics exhibit upper and lower stable fixed points separated by an unstable threshold. The underlying bistability of the stochastic theory allows large initial populations of the asymmetric species to remain dominant on intermediate time scales, but large fluctuations below the unstable threshold rapidly reduce mean times to extinction. Only intraspecific exceeding interspecific competition raises $\tau_E$ above neutral expectations for all values of $p_{10}$. The corresponding mean dynamics include a stable fixed point that promotes stable coexistence over intermediate time scales as well as an unstable fixed point that repels drift toward extinction. We expect niche stabilization to generate reasonable species lifetimes in non-neutral metacommunities and restore Hubbell’s point-speciation mechanism as a viable phenomenological model.

**Niche stabilization of Hubbell’s local community**

We now expand on an asymmetric extension of Hubbell’s local community theory, as described in Box 2, by allowing for density-dependence in ecological fitness. The master equation is given by Eq. B2.3 with the replacement of each $w_i$ by $w_{i-\bar{r}}$. The simple Moran model is recovered in the limit where all immigration probabilities vanish, and the multivariate formulation of Hubbell’s local community theory (Hubbell, 2001, p. 128) is included as the symmetric limit. The mean dynamics approximating our non-neutral local community dynamics can be written as a Levins model, and we assume weak competitive asymmetries to obtain

$$
\frac{dp_i}{d\tau} = s_i(\vec{p}) + c_i(\vec{p})p_i (1 - p_i) - e(\vec{p})p_i - \sum_{j=1,j\neq i}^S c_j(\vec{p})p_i p_j,
$$

(21)
Figure 3: Panel a plots mean times to extinction, $\tau_E$, against initial relative abundance, $p_{10} \equiv n_{10}/J_M$, for the asymmetric species in a nearly neutral metacommunity with $J_M = 100$ individuals, while panel b plots the corresponding flows, $dp_1/d\tau$ versus $p_1$, of the mean dynamics. We assume equivalence in speciation probability, with $\nu_1 = \nu_2 = 0.01$, and intrinsic ecological fitness, such that $w_{10} = w_{20}$. In the fully neutral limit, where $a_{1j} = a_{2j}$ for $j = 1, 2$, all species drift steadily toward extinction. For the case of interspecific exceeding intraspecific competition, where $a_{11}, a_{22} = 0.1/J_M < a_{21}, a_{12} = 0.2/J_M$, mean time to extinction for the asymmetric species falls below (above) neutral expectations when relative abundance is low (high). The existence of an inflection point in the $\tau_E$ versus $p_{10}$ curve signals a stochastic Allee effect, as confirmed by the mean dynamics where an unstable threshold separates an upper and a lower stable fixed point. Only intraspecific exceeding interspecific competition, where $a_{11}, a_{22} = 0.2/J_M > a_{21}, a_{12} = 0.1/J_M$, raises $\tau_E$ above neutral expectations for all values of $p_{10}$. The corresponding mean dynamics include a stable fixed point that promotes stable coexistence over intermediate time scales as well as an unstable fixed point that repels drift toward extinction.
where

\[
\begin{align*}
s_i(\vec{p}) &= \frac{m_i \ w_i(\vec{p}) x_i}{J_L \sum_{k=1}^{S} w_k(\vec{p}) x_k}, \\
c_i(\vec{p}) &= \frac{1 - m_i \ w_i(\vec{p})}{J_L \sum_{k=1}^{S} w_k(\vec{p}) p_k}, \\
e(\vec{p}) &= \sum_{j=1}^{S} \frac{m_j \ w_j(\vec{p}) x_j}{J_L \sum_{k=1}^{S} w_k(\vec{p}) x_k}.
\end{align*}
\]

(22)

Here, the source and extinction terms arise from nonzero immigration probabilities. The mean dynamics of Eq. 21 approximate non-neutral local community dynamics given any fixed number of species and individuals. In the neutral limit, we have (Vallade & Houchmandzadeh, 2003)

\[
\frac{d p_i}{d \tau} = m_i \ J_L (x_i - p_i),
\]

(23)
such that all species completely decouple and local relative community abundances track relative metacommunity abundances at equilibrium. Similarly, in the stochastic formulation of Hubbell’s local community, the expected relative abundance of species \(i\) is \(x_i\) at equilibrium (Hubbell, 2001). This provides a built-in mechanism for stabilizing coexistence: given a nonzero probability of immigration, high levels of diversity in the metacommunity guarantee high levels in the local community when abundances are averaged over long time scales. However, low immigration probabilities generate large fluctuations that destabilize local diversity on shorter time scales and prolong periods of extirpation. Expanding the equilibrium expression for relative fluctuation amplitude in Hubbell’s theory (Vallade & Houchmandzadeh, 2003), we find (see SI.8)

\[
\sqrt{\frac{\langle N_i - \langle N_i \rangle \rangle^2}{\langle N_i \rangle}} = \frac{1}{\sqrt{J_L}} \sqrt{\frac{1 - x_i}{m x_i}} + O(J_L^{-3/2}),
\]

(24)
so, for sufficiently small values of \(m\), population fluctuations equal to the total number of individuals in the community become common, which implies a bimodal stationary distribution with peaks at extirpation and monodominance.

Our non-neutral framework extends Hubbell’s theory to allow for a niche mechanism that, despite low levels of immigration, promotes coexistence and shortens periods of extirpation. To demonstrate this, we calculate a stationary distribution, \(P_{n_1}^*\), for the asymmetric species in a nearly neutral local community (see SI.9). Averaging over long-term stochastic fluctuations, the relative amount of time that the asymmetric species spends in state \(n_1\) is equal to \(P_{n_1}^*\). Given \(m_1 = m_2 \ll 1\), Fig. 4a plots stationary distributions for the asymmetric species in three scenarios, while Fig. 4b plots corresponding...
Figure 4: Stationary distributions, $P^*_n$, (panel a), and corresponding flows in the mean dynamics, $dp_1/d\tau$ (panel b), for the asymmetric species in a nearly neutral local community of $J_L = 100$ individuals. The relative metacommunity abundance is $x_1 = 0.25$; the migration probabilities are symmetric with $m_1 = m_2 = 0.01$; and intrinsic ecological fitnesses are equivalent, such that $w_{10} = w_{20}$. In the fully neutral limit, the stationary distribution is bimodal and large fluctuations between extirpation and monodominance destabilize the community. Probabilities of coexistence decline further when interspecific exceeds intraspecific competition, such that $a_{11}, a_{22} = 0.1/J_M < a_{21}, a_{12} = 0.2/J_M$, and the mean dynamics exhibit an Allee effect. By contrast, intraspecific exceeding interspecific competition such that $a_{11}, a_{22} = 0.2/J_M > a_{21}, a_{12} = 0.1/J_M$, generates a metastability at intermediate abundance that fosters coexistence over intermediate time scales and delays extirpation. That metastability corresponds to a stable fixed point in the mean dynamics, where flows away from extirpation and monodominance further reduce the probability of large fluctuations.
flows in the mean dynamics. In the fully neutral limit, the stationary distribution is bimodal with peaks at extirpation and monodominance, and low probabilities of coexistence. When interspecific exceeds intraspecific competition, the mean dynamics exhibit an Allee effect where the unstable threshold at intermediate abundance corresponds to a further reduction in probabilities of coexistence for the stationary distribution (Dennis, 1989). By contrast, intraspecific exceeding interspecific competition induces a tri-stable distribution with a metastability for coexistence that reduces periods of extirpation and monodominance. That metastability corresponds to a stable fixed point of the mean dynamics, and for low levels of immigration, stability criteria are well-approximated by results for the simple Moran model (see SI.6).

Discussion

In his influential review of mechanisms for the maintenance of species diversity, Chesson (2000) notes that, “Models of unstable coexistence, in which species diversity slowly decays over time, have focused almost exclusively on equalizing mechanisms. These models would be more robust if they also included stabilizing mechanisms, which arise in many and varied ways but need not be adequate for full stability of a system. Models of unstable coexistence invite a broader view of diversity maintenance incorporating species turnover”. With the simple introduction of asymmetries in density-dependent ecological fitnesses, our niche stabilization of Hubbell’s theory offers a remarkably economical approach to embedding stabilizing mechanisms within a neutral model of unstable coexistence. This nested framework not only presents the first parameteric model for estimating the relative importance of niche versus neutral dynamics based on empirical data, but also delivers the first mechanistic metacommunity model to quantify the impact of competition on extinction. We have demonstrated that niche stabilization prolongs species lifetimes and may revive Hubbell’s point-speciation mechanism as a viable phenomenological model. These results underscore the ecological importance of multiple time scales and extended transients, as emphasized by Hastings (2004).

Much of the controversy surrounding Hubbell’s theory centers on the assumption of per capita equivalence in ecological fitness (see, e.g., Leibold & McPeek (2006)). What equalizing mechanisms might generate neutrality? Hubbell (2001) argued that life-history tradeoffs constrain niche differentiation to fitness-invariant manifolds. In our non-neutral framework, Hubbell’s theory lies along hyperplanes of parameter space where \( w_i = w \) and \( a_{ij} = a_j \) for all \( i \) and \( j \). In this context, broad questions over the evolution of neutrality boil down to a search for mechanisms that equalize both the intrinsic ecological fitness of each species and the interaction strength of any given species.
with itself and all others. Toward this end, future work should integrate mechanistic models of niche stabilization, such as the consumer-resource models of Tilman (1980, 1982), into a stochastic theory of unstable coexistence.

Many additional directions in model-building remain to be explored. The work of Melbourne & Hastings (2008) highlights the need to move beyond considerations of purely demographic stochasticity to incorporate explicit, parametric models of environmental stochasticity and demographic heterogeneity, among other sources of variation. O’Dwyer et al. (2009) have integrated size-structure into Hubbell’s theory, and our non-neutral model of unstable coexistence might be expanded in similar ways. Further efforts should also be made to incorporate niche stabilization into spatially explicit models of unstable coexistence. Incorporating space into Hubbell’s theory has generated analytical predictions for clustering (Houchmandzadeh & Vallade, 2003), beta-diversity (Chave & Leigh, 2002; Zillio et al., 2005), and a tri-phasic species-area relationship (O’Dwyer & Green, 2010). Others developments by Economo & Keitt (2008), Muneepakul et al. (2008), Babak & He (2009), and Vanpeteghem & Haegeman (2010) implement neutral dynamics over a distributed network of patches. These efforts should be expanded to incorporate asymmetries and the mechanisms of niche stabilization. Advances in stochastic modeling, both spatially-explicit and spatially-implicit, may provide novel insights on the early warning signals of extinction in deteriorating environments, as studied empirically by Drake & Griffen (2010).

The successes of neutral theory have led to suggestions that emergent regularities, such as unimodal RSA distributions, imply a simplicity in the underlying dynamics of ecological communities. But increasingly, the opposite perspective is receiving attention. Can we embrace the complexity of community dynamics at the level of individuals and perform scaling operations to demonstrate a robustness in the predictions of large-scale patterns of diversity? In physics, the simplicity of Coulomb’s law over macroscopic distances emerges from a complex web of fundamental particles interacting over microscopic scales. Nonlinear interactions decouple at longer length scales and endow our everyday world with a measure of predictability. Application of the appropriate theoretical tools in ecology may yield scalings that generate biogeographic regularity from a complex web of interacting individuals.
Box 1: Limit cycles

If we consider Eq. 8 as a prescription for two-species predator-prey dynamics, a stable, self-sustaining limit cycle may arise, as shown in Fig. B.1. Although stable limit cycles can be found in two-species systems with a functional response (see, e.g., Kot (2001)), they do not occur in the two-species classical niche model (Hastings, 1978), which, as noted above, approximates the dynamics of Eq. 8 when abundances are sufficiently small. In fact, our numerical work indicates that the stable limit cycle of Fig. B.1 vanishes when the exponential of density-dependent ecological fitness is approximated by a truncated power series of any order.

Figure B.1: The dark loop traces a stable limit cycle in two-species predator-prey dynamics as prescribed by Eq. 8. The abundances of prey and predator are \( n_1 \) and \( n_2 \), respectively. The parameters are \( w_{10} = 0.11, d_1 = 0.1, a_{11} = -0.05, \) and \( a_{12} = 0.2 \) for the prey, and \( w_{20} = 0.1, d_2 = 0.2, a_{22} = 0.05, \) and \( a_{21} = -0.1 \) for the predator. Two trajectories attracted to the limit cycle are drawn in gray. Stable limit cycles do not exist in two-species predator-prey systems of the classical niche model, although they can be found in extensions that include a functional response (see, e.g., Kot (2001)).
Box 2: An asymmetric extension of Hubbell’s neutral theory

Previous work, in collaboration with Nico Temme and Tim Keitt, introduced an analytical model of asymmetric, zero-sum community dynamics that contains Hubbell’s neutral theory of biodiversity in the symmetric limit [Noble et al., 2011]. Our asymmetric metacommunity \((M)\) retains Hubbell’s point-speciation model but allows for variation in ecological fitnesses, the \(w_i\), and speciation probabilities, the \(\nu_i\), across species. Dynamics are governed by the master equation

\[
\frac{dP^M}{d\tau} = \sum_{i=1}^{S} \sum_{j=1, j \neq i}^{S} \left( T^M_{ij\vec{n} + \vec{e}_i - \vec{e}_j} P^M_{\vec{n} + \vec{e}_i - \vec{e}_j} - T^M_{ji\vec{n}} P^M_{\vec{n}} \right) \Theta^M_{ij},
\]

(B2.1)

where \(S\) is the total number of possible species, \(\tau\) is a dimensionless measure of time, the \(\vec{e}_i\) are \(S\)-dimensional unit vectors, and the

\[
T^M_{ij\vec{n}} = \frac{n_i}{J_M} \left( 1 - \nu_j \right) \frac{w_j n_j}{\sum_{k=1}^{S} w_k n_k - w_i} + \nu_j \frac{w_j}{\sum_{k=1}^{S} w_k} + O\left( \frac{1}{S} \right),
\]

(B2.2)

are one-step transition probabilities for the removal of species \(i\) followed by the addition of species \(j\), where \(O(1/S)\) indicates the presence of additional terms that are negligible as the number of species becomes large. The number of individuals, \(J_M\), is fixed, and the accessible states are abundances vectors, \((n_1, \ldots, n_S)\), where \(\sum_{i=1}^{S} n_i = J_M\) and \(0 \leq n_i \leq J_M\). The \(\Theta^M_{ij} = \Theta(J_M - (n_i + 1))\Theta(n_j - 1)\), where \(\Theta(x)\) is zero for \(x < 0\) and one otherwise, ensure that transitions to inaccessible states are not included in Eq. (B2.1). Note the absence of absorbing states: species have nonzero probabilities of re-introduction following an extinction event. However, as the number of possible species becomes appropriately large, the probability of re-introduction becomes vanishingly small.

Our asymmetric local community \((L)\) allows for variation in ecological fitnesses, the \(w_i\), and immigration probabilities, the \(m_i\), given fixed relative metacommunity abundances, the \(x_i\). Dynamics are governed by the multivariate master equation

\[
\frac{dP^L}{d\tau} = \sum_{i=1}^{S} \sum_{j=1, j \neq i}^{S} \left( T^L_{ij\vec{n} + \vec{e}_i - \vec{e}_j} P^L_{\vec{n} + \vec{e}_i - \vec{e}_j} - T^L_{ji\vec{n}} P^L_{\vec{n}} \right) \Theta^L_{ij},
\]

(B2.3)

where

\[
T^L_{ij\vec{n}} = \frac{n_i}{J_L} \left( 1 - m_j \right) \frac{w_j n_j}{\sum_{k=1}^{S} w_k n_k - w_i} + m_j \frac{w_j x_j}{\sum_{k=1}^{S} w_k x_k}.
\]

(B2.4)
The number of individuals, $J_L$, is fixed, and the accessible states are abundance vectors, $(n_1, \ldots, n_S)$, where $\sum_{i=1}^{S} n_i = J_L$ and $0 \leq n_i \leq J_L$. The $\Theta_{ij} = \Theta(J_L - (n_i + 1))\Theta(n_j - 1)$ ensure that transitions to inaccessible states are not included in Eq. B2.3. Nonzero values for the $m_i$ guarantee the absence of absorbing states and promote coexistence via mass-effects. In Hubbell’s neutral theory, at equilibrium, expected relative abundances in the local community equal relative abundances in the metacommunity. By introducing asymmetries in ecological fitness and migration probability, our asymmetric theory allows the expected local community composition to differ from the metacommunity composition.

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**Supporting Information**

**SI.1. Mean dynamics**

According to Eq. 3.5.14 of Gardiner (2004), the mean dynamics of a multivariate Markov process is a system of ordinary differential equations given by

$$\frac{dn_i}{dt} = A_i,$$

(SI.1.1)

for each species $i$, where $n_i$ is promoted from a discrete index to a continuous variable and

$$A_i + O(\epsilon) = \lim_{\Delta t \to 0} \frac{1}{\Delta t} \int_{|\vec{m} - \vec{n}| < \epsilon} d\vec{m} \ (m_i - n_i)P \left( \vec{N}(t + \Delta t) = \vec{m} | \vec{N}(t) = \vec{n} \right),$$

(SI.1.2)

are the first-order jump moments as defined by Eq. 3.4.2 of Gardiner (2004). For the transition probabilities of Eq. 7 we find

$$P \left( \vec{N}(t + \Delta t) = \vec{m} | \vec{N} = \vec{n}(t) \right) = \sum_{j=1}^{S} \left( \delta((\vec{m} + \vec{e}_j) - \vec{n})g_{ji} + \delta((\vec{m} - \vec{e}_j) - \vec{n})r_{ji} \right) \Delta t + o(\Delta t),$$

(SI.1.3)
so
A_i = g_{i\vec{n}} - r_{i\vec{n}}, \quad (SI.1.4)

and Eq. SI.1.1 yields Eq. 8. For the transition probabilities of Eq. 12, we find

\[ P \left( \vec{N}(\tau + \Delta \tau) = \vec{m} | \vec{N} = \vec{n}(\tau) \right) = \sum_{k=1}^{S} \sum_{j=1, j \neq k}^{S} \left( \delta((\vec{m} - \vec{e}_j + \vec{e}_k) - \vec{n})T_{jk\vec{n}} + \delta((\vec{m} - \vec{e}_k + \vec{e}_j) - \vec{n})T_{kj\vec{n}} \right) \Delta \tau + o(\Delta \tau), \]

so

\[ A_i = \sum_{j=1, j \neq i}^{S} (T_{ji\vec{n}} - T_{ij\vec{n}}), \quad (SI.1.5) \]

and Eq. SI.1.1 with \( t \to \tau \), yields Eq. 13, given \( p_i \equiv n_i / J \) and the assumption of sufficiently weak competitive asymmetry such that \( w_{i\vec{n}} \ll \sum_{k=1}^{S} w_{k\vec{n}n_k} \) and \( a_{ij} \ll \sum_{k=1}^{S} a_{ik}n_k \) for every \( i \) and \( j \). A Kramers-Moyal expansion or Van Kampen system size expansion yields mean dynamics identical to the ones derived here (see the discussion in Gardiner (2004, p. 251)).

**SI.2. Obtaining the Ricker model from the mean dynamics of a simple birth-death process**

Eq. 8 prescribes the single-species dynamics

\[ \frac{dn_1}{dt} = n_1(w_{10}e^{-a_{11}n_1/w_{10}} - d_1). \]

Let \( \tau = d_1 t \) and discretize the derivative to obtain

\[ n_{1\tau+1} = n_{1\tau} + n_{1\tau}\left( \frac{w_{10}}{d_1} e^{-a_{11}n_{1\tau}/w_{10}} - 1 \right), \]

\[ = n_{1\tau}e^{r(1-n_{1\tau}/K)}, \quad (SI.2.2) \]

where

\[ r = \log(w_{10}/d_1), \]

\[ K = \frac{w_{10}}{a_{11}} \log(w_{10}/d_1). \]

Eq. SI.2.2 is the Ricker model.
SI.3. The mean dynamics of a Moran model retains the zero-sum rule

Summing Eq. 13 over all species, we obtain

$$\sum_{i=1}^{S} \frac{dp_i}{d\tau} = \sum_{i=1}^{S} c_i p_i \left(1 - \sum_{j=1}^{S} p_j\right).$$  \hspace{1cm} \text{(SI.3.1)}$$

If \(\sum_{j=1}^{S} p_i(0) = 1\), then \(\sum_{i=1}^{S} p_i(\tau)|_{\tau=0} = 0\), which is sufficient to guarantee that \(\sum_{j=1}^{S} p_i(\tau) = 1\) for all \(\tau\).

SI.4. Numerical integration of the probability distributions in a simple Moran model

In the \(S = 2\) case of Eq. 11, the stochastic dynamics can be written, without approximation, as a univariate master equation for the marginal distribution of the first species

$$\frac{P_{n_1}}{d\tau} = g_{n_1-1} \Theta(n_1 - 1) P_{n_1-1} + r_{n_1+1} \Theta(J - (n_1 + 1)) P_{n_1+1}$$

$$- g_{n_1} \Theta(J - (n_1 + 1)) P_{n_1} + r_{n_1} \Theta(n_1 - 1) P_{n_1},$$ \hspace{1cm} \text{(SI.4.1)}$$

with

$$g_{n_1} \equiv T_{12(n_1,n_2)}$$

$$= \frac{J - n_1}{J} \left(\frac{e^{-(B_1+B_2)n_1/J-B_2-a_{12}/w_{10}+a_{22}/w_{20})n_1}{e^{-(B_1+B_2)n_1/J-B_2-a_{12}/w_{10}+a_{22}/w_{20})n_1 + J - n_1 - 1}\right),$$

$$r_{n_1} \equiv T_{12(n_1,n_2)}$$

$$= \frac{n_1}{J} \left(\frac{J - n_1}{e^{-(B_1+B_2)n_1/J-B_2+a_{21}/w_{20}-a_{11}/w_{10})(n_1 - 1) + J - n_1}\right).$$ \hspace{1cm} \text{(SI.4.2)}$$

This master equation also governs marginal dynamics for the asymmetric species in a nearly neutral community where all other species, labelled 2 thru \(S\), are symmetric (see Noble et al. (2011)).

To calculate the temporal evolution of conditional abundance probability distributions, as plotted in Fig. 1, we start by discretizing the univariate birth-death process of Eq. 1.1 to obtain

$$P_{n_1,\tau+1} = g_{n_1-1} \Theta(n_1 - 1) P_{n_1-1,\tau} + r_{n_1+1} \Theta(J - (n_1 + 1)) P_{n_1+1,\tau}$$

$$+ (1 - g_{n_1} \Theta(J - (n_1 + 1)) - r_{n_1} \Theta(n_1 - 1)) P_{n_1,\tau}$$

$$= \sum_{m=0}^{J} P_{m,\tau} W_{mn_1},$$ \hspace{1cm} \text{(SI.4.3)}$$
where

\[
W = \begin{pmatrix}
1 - g_0 & g_0 & 0 & \cdots & 0 & 0 & 0 \\
r_1 & 1 - r_1 - g_1 & g_1 & \cdots & 0 & 0 & 0 \\
\vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\
0 & 0 & 0 & \cdots & r_{J-1} & 1 - r_{J-1} - g_{J-1} & g_{J-1} \\
0 & 0 & 0 & \cdots & 0 & r_J & 1 - r_J
\end{pmatrix}.
\] (SI.4.4)

The unconditioned abundance probability distribution at any integer time \(\tau\), denoted \(\vec{P}_\tau\), is given by

\[
\vec{P}_\tau = \vec{P}_0 W^\tau.
\] (SI.4.5)

The abundance probability distribution conditioned against extinction and monodominance is

\[
P_{cn_1,\tau} \equiv \frac{P_{n_1,\tau}}{1 - P_{0,\tau} - P_{J,\tau}},
\] (SI.4.6)

for \(n_1 = 1, \ldots, J - 1\).

**SI.5. Recovering ordinary dynamics from zero-sum dynamics**

Our general approach is to treat empty space as the \((S+1)\)th species in a community of \(S\) species. Let \(w_{(S+1)0}\) be the rate at which death events generate empty space and set all the \(a_{ij}\) to zero for \(i, j = S + 1\). Given this setup, we consider the dynamics of a large-\(J\) community as \(n_{S+1} \to J\).

Starting from the master equation for the Moran model in Eq. [11], we find

\[
T_{iS+10} \sim \frac{n_i}{J},
\]

\[
T_{S+1i0} \sim \frac{w_{i0}}{w_{(S+1)0}} \frac{n_i}{J},
\] (SI.5.1)

and all other transition probabilities are higher-order in \(n_i/J\) for \(i \neq S + 1\). Now let \(r\) be the overall transition rate. Rescaling \(w_{i0} \to w_{(S+1)0}w_{i0}/r\), setting \(\tau = rJt\), and identifying \(T_{S+1i}\) and \(T_{iS+1}\) with \(g_{i0}\) and \(r_{i0}\), respectively, we find that Eq. [11] reduces to Eq. [6] with \(d_i = r\).

Starting from the mean dynamics of the Moran model in Eq. [13] and using \(p_i = n_i/J\), we find

\[
\frac{dn_i}{d\tau} \sim \frac{w_{i0}}{w_{(S+1)0}} \frac{n_i}{J} - \frac{n_i}{J},
\] (SI.5.2)

with all other terms being higher-order in \(n_i/J\) for \(i \neq S + 1\). The same rescalings as before yield Eq. [8] with \(d_i = r\).
SI.6. Corrections to stability criteria of the simple Moran model for low levels of speciation and migration

In a nearly neutral metacommunity where only the first species is distinct in ecological function, parameters for the symmetric species are identical: \( w_{i0} = w_{20} \) and \( a_{ij} = a_{2j} \) for all \( i > 1 \) and all \( j \). If the number of symmetric species, \( S - 1 \), is large such that terms of \( \mathcal{O}(S) \) can be ignored in Eq. 18, then the mean dynamics for the asymmetric species can be written as

\[
\frac{dp_1}{d\tau} = \frac{1}{J_M} \frac{(1 - \nu_1)e^{-((B_1+B_2)p_1-B_2)} - (1 - \nu_2)}{e^{-((B_1+B_2)p_1-B_2)}p_1 + 1 - p_1} p_1 (1 - p_1) - \frac{\nu_2}{J_M} p_1,
\]

where \( B_1 \) and \( B_2 \) are given by Eq. 16 with the substitution \( J \to J_M \). The stable fixed point of the nearly neutral metacommunity can be calculated perturbatively in \( \nu_1 \) and \( \nu_2 \). At leading order, we find

\[
p_1^* = \frac{B_2 - C_{\nu_1} \nu_1 - C_{\nu_2} \nu_2}{B_1 + B_2} + \mathcal{O}(\nu_1^2, \nu_2^2, \nu_1 \nu_2),
\]

\[
p_{i>1}^* = \frac{1 - p_1^*}{S - 1},
\]

where

\[
C_{\nu_1} = 1,
\]

\[
C_{\nu_2} = \frac{B_2}{B_1}.
\]

Stability requirements can be found from the linearization

\[
\frac{dp_1}{d\tau} = \frac{1}{J_M} \frac{(B_1 + D_{\nu_1} \nu_1)(B_2 + D_{\nu_2} \nu_2)}{B_1 + B_2} (p_1 - p_1^*) + \mathcal{O}(\nu_1^2, \nu_2^2, \nu_1 \nu_2),
\]

where

\[
D_{\nu_1} = \frac{B_2^2 - B_1^2 - B_1 B_2^2}{B_2 (B_1 + B_2)},
\]

\[
D_{\nu_2} = \frac{B_2}{B_1} \left( \frac{2 - \frac{B_1 B_2}{B_1 + B_2}}{2} \right).
\]

For a nearly neutral local community, the dynamics of the asymmetric species, as prescribed by Eq. 21, can be written as

\[
\frac{dp_1}{d\tau} = \frac{1}{J_M} \frac{(1 - \nu_1)e^{-((B_1+B_2)p_1-B_2)} - (1 - \nu_2)}{e^{-((B_1+B_2)p_1-B_2)}p_1 + 1 - p_1} p_1 (1 - p_1) - \frac{\nu_2}{J_M} p_1,
\]

27
where $B_1$ and $B_2$ are given by Eq. 16 with the substitution $J \to J_L$. The stable fixed point of the nearly neutral local community can be calculated perturbatively in $m_1$ and $m_2$. At leading order, we find

\[
p_1^* = \frac{B_2 - C_{m_1} m_1 - C_{m_2} m_2}{B_1 + B_2} + \mathcal{O}(m_1^2, m_2^2, m_1 m_2),
\]

\[
p_{i>1}^* = 1 - p_i^* S - \frac{1}{S - 1},
\]

(SI.6.7)

where

\[
C_{m_1} = 1 - x_1 \frac{B_1 + B_2}{B_2},
\]

\[
C_{m_2} = \frac{B_2}{B_1} - x_1 \frac{B_1 + B_2}{B_1}.
\]

(SI.6.8)

Stability requirements can be found from the linearization

\[
\frac{dp_1}{d\tau} = -\frac{1}{J_L} \frac{(B_1 + D_{m_1} m_1)(B_2 + D_{m_2} m_2)}{B_1 + B_2} (p_1 - p_1^*) + \mathcal{O}(m_1^2, m_2^2, m_1 m_2),
\]

(SI.6.9)

where

\[
D_{m_1} = \frac{1}{B_2^2 (B_1 + B_2)} \left( B_2^3 (1 - x_1) + 2 B_1^2 B_2^2 x_1 (1 - x_1) - B_1 B_2 (B_1 + B_2) (1 - x_1)^2 - 3 B_1 x_1 (2 - B_2 x_1) \right),
\]

\[
D_{m_2} = \frac{1}{B_1^2 (B_1 + B_2)} \left( 2 B_2^3 (1 - x_1) + 2 B_1^2 B_2^2 x_1 (1 - x_1) + B_1 B_2^2 (2 - B_2 (1 - x_1)^2 - 3 x_1) + B_1^3 x_1 (1 - B_2 x_1) \right).
\]

(SI.6.10)

SI.7. Calculation of extinction times in a nearly neutral metacommunity

If we assume a sufficiently large number of symmetric species such that $\mathcal{O}(1/S)$ terms in the master equation are negligible, marginal dynamics for the asymmetric species are governed by Eq. SI.4.1 with

\[
g_{n_1} = \frac{J_M - n_1}{J_M} \left( (1 - \nu_1) e^{-((B_1 + B_2) n_1 / J_M - B_2 - a_{12}/w_{10} + a_{22}/w_{20}) n_1} + J_M - n_1 - 1 \right),
\]

\[
r_{n_1} = \frac{n_1}{J_M} \left( (1 - \nu_2) e^{-((B_1 + B_2) n_1 / J_M - B_2 + a_{11}/w_{10}) n_1} + J_M - n_1 + \nu_2 \right),
\]

(SI.7.1)
where $B_1$ and $B_2$ are given by Eq. [16] with the substitution $J \rightarrow J_M$. Hubbell’s univariate metacommunity dynamics (Hubbell 2001) are included as the fully symmetric limit. For an initial abundance of $n_{10}$, the mean times to extinction, $\tau_E$, are calculated using (Gardiner 2004, p. 260)

$$\tau_E = \sum_{p=0}^{n_{10}-1} \phi^M_p \sum_{q=p+1}^{J_M-1} \frac{1}{g^M_q \phi^M_q},$$

(SI.7.2)

where $\phi^M_0 = 1$ and for $p > 0$

$$\phi^M_p = \prod_{m=1}^{p} \frac{r^M_m}{g^M_m}.$$ 

(SI.7.3)

**SI.8. Fluctuations in large local communities**

In Hubbell’s theory of local communities, the expected abundance of each species at equilibrium is

$$\lim_{\tau \to \infty} \langle N_i(\tau) \rangle = x_i J_L.$$ 

(SI.8.1)

Vallade & Houchmandzadeh (2003) first calculated the variance at equilibrium

$$\lim_{\tau \to \infty} \langle (N_i(\tau) - \langle N_i(\tau) \rangle)^2 \rangle = x_i (1 - x_i) J_L \left( \frac{J_L + I}{1 + I} \right),$$

(SI.8.2)

where $I = (J_L - 1)m/(1 - m)$ is called the “fundamental dispersal number” (Etienne & Alonso 2005). Then, for large $J_L$, we obtain the approximation in Eq. 24.

**SI.9. A stationary distribution for the asymmetric species in a nearly neutral local community with weak competitive interactions**

Marginal dynamics for the asymmetric species are governed by Eq. [SI.4.1] with

$$g_{n_1} = \frac{J_L - n_1}{J_L} \left( (1 - m_1) \frac{\rho_g(n_1)n_1}{\rho_g(n_1)n_1 + J_L - n_1 - 1} + m_1 \frac{\rho_g(n_1)x_1}{\rho_g(n_1)x_1 + 1 - x_1} \right),$$

$$r_{n_1} = \frac{n_1}{J_L} \left( (1 - m_2) \frac{J_L - n_1}{\rho_r(n_1)(n_1 - 1) + J_L - n_1} + m_2 \frac{1 - x_1}{\rho_r(n_1)x_1 + 1 - x_1} \right),$$

(SI.9.1)

where

$$\rho_g(n_1) = e^{-((B_1 + B_2)n_1/J_L - B_2 - a_{12}/w_{10} + a_{22}/w_{20})},$$

$$\rho_r(n_1) = e^{-((B_1 + B_2)n_1/J_L - B_2 + a_{21}/w_{20} - a_{11}/w_{10})}.$$ 

(SI.9.2)
and $B_1$ and $B_2$ are given by Eq. [16] with the substitution $J \rightarrow J_L$. We now assume weak competitive interactions such that

$$
\rho_g(n_1) \sim 1 - ((B_1 + B_2)n_1/J_L - B_2 - a_{12}/w_{10} + a_{22}/w_{20})
\equiv c_g + d n_1,
$$

$$
\rho_r(n_1) \sim 1 - ((B_1 + B_2)n_1/J_L - B_2 + a_{21}/w_{20} - a_{11}/w_{10})
\equiv c_r + d n_1,
$$

where

$$
c_g = 1 + \log \left( \frac{w_{10}}{w_{20}} \right) + (J_L - 1) \frac{a_{22}w_{10} - a_{12}w_{20}}{w_{10}w_{20}},
$$

$$
c_r = 1 + \log \left( \frac{w_{10}}{w_{20}} \right) + J_L \frac{a_{22}w_{10} - a_{12}w_{20}}{w_{10}w_{20}} + \frac{a_{11}w_{20} - a_{21}w_{10}}{w_{10}w_{20}},
$$

$$
d = - \frac{w_{10}(a_{22} - a_{21}) + w_{20}(a_{11} - a_{12})}{w_{10}w_{20}}. \tag{SI.9.4}
$$

We specialize to the case where $a_{11} = a_{22}$, $a_{12} = a_{21}$, and $w_{10} = w_{20}$, so that $c_g = c_r \equiv c$. The stationary distribution, $P_{n_1}^* \equiv \lim_{\tau \rightarrow \infty} P_{n_1}(\tau)$, is given by a well-known formula

$$
P_{n_1}^* = P_0^* \prod_{i=0}^{n_1-1} \frac{g_i}{r_{i+1}}. \tag{SI.9.5}
$$

After some algebra, we obtain the closed form

$$
P_{n_1}^* \equiv Z \left( \frac{J_L}{n_1} \right) \left( 1 + \frac{x(c + d n_1)}{1 - x} \right) \eta^{n_1}(c/d)_{n_1}
\times \frac{B(\lambda_{a+} + n_1, \xi_{a+} - n_1)B(\lambda_{a-} + n_1, \xi_{a-} - n_1)}{B(\lambda_{a+}, \xi_{a+})B(\lambda_{a-}, \xi_{a-})}
\times \frac{B(\lambda_{b+} + n_1, \xi_{b+} - n_1)B(\lambda_{b-} + n_1, \xi_{b-} - n_1)}{B(\lambda_{b+}, \xi_{b+})B(\lambda_{b-}, \xi_{b-})}, \tag{SI.9.6}
$$

where $(y)_z \equiv \Gamma(y + z)/\Gamma(y)$ is the Pochhammer symbol, $B(y, z) = \Gamma(y + z)/\Gamma(y)\Gamma(z)$ is the Beta function, and

$$
Z^{-1} = {}_6F_4(-J_L, c/d, \lambda_{a+}, \lambda_{a-}, \lambda_{b+}, \lambda_{b-}; 1 - \xi_{a+}, 1 - \xi_{a-}, 1 - \xi_{b+}, 1 - \xi_{b-}; -\eta)
+ xc \ {}_6F_4(-J_L, c/d + 1, \lambda_{a+}, \lambda_{a-}, \lambda_{b+}, \lambda_{b-}; 1 - \xi_{a+}, 1 - \xi_{a-}, 1 - \xi_{b+}, 1 - \xi_{b-}; -\eta), \tag{SI.9.7}
$$

30
and

\[
\begin{align*}
\lambda_{a\pm} &= \frac{1}{2d} \left( c + d - 1 \pm \sqrt{(1 - c + d)^2 - 4d(J_L - 1)} \right), \\
\lambda_{b\pm} &= \frac{1}{2dx} \left( 1 - m - x + cx \pm \sqrt{(1 - m - x + cx)^2 - 4mdx^2(J_L - 1)} \right), \\
\xi_{a\pm} &= \frac{1}{2d} \left( 1 - c + 2d \pm \sqrt{(1 - c)^2 - 4d(J_L - 1)} \right), \\
\xi_{b\pm} &= \frac{1}{2d(m_2 - x)} \left( 1 + (d - c)m_2 - (d - c + 1)x - (1 - m_2)dx(J_L - 1) \right. \\
&\quad \left. \pm \sqrt{(1 - (d + c)m_2 + (d + c - 1)x - (1 - m_2)dx(J_L - 1))^2} \cdots \\
&\quad \cdots - 4(J_L - 1)d(m_2 - x)(x + x(c + d)(m_2 - 1) - 1) \right), \\
\eta &= \frac{dx}{m_2 - x}.
\end{align*}
\]

Eq. SI.9.6 is a generalized hypergeometric distribution \cite{Kemp1968, Johnson1992}.

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