Phenomenology and dynamics of competitive ecosystems beyond the niche-neutral regimes

Nava Leibovich1,2, Jeremy Rothschild3, Sidhartha Goyal4,5, and Anton Zilman1,2

Edited by Pablo Marquet, Pontificia Universidad Católica de Chile, Santiago, Chile; received March 12, 2022; accepted September 18, 2022

Structure, composition, and stability of ecological populations are shaped by the inter- and intraspecies interactions within their communities. It remains to be fully understood how the interplay of these interactions with other factors, such as immigration, controls the structure, the diversity, and the long-term stability of ecological systems in the presence of noise and fluctuations. We address this problem using a minimal model of interacting multispecies ecological communities that incorporates competition, immigration, and demographic noise. We find that a complete phase diagram exhibits rich behavior with multiple regimes that go beyond the classical “niche” and “neutral” regimes, extending and modifying the “rare biosphere” or “niche-like” dichotomy. In particular, we observe regimes that cannot be characterized as either niche or neutral where a multimodal species abundance distribution is observed. We characterize the transitions between the different regimes and show how these arise from the underlying kinetics of the species turnover, extinction, and invasion. Our model serves as a minimal null model of noisy competitive ecological systems, against which more complex models that include factors such as mutations and environmental noise can be compared.

Composition and behavior of ecological communities are shaped by direct and indirect interactions between the occupant species, such as the competition for the physical space and the intrinsic and extrinsic resources. Examples of such competitive ecosystems are microbial communities in various biomes such as the soil (1), the ocean (2, 3), and the human body (4)—in particular, the human gut, which hosts a diverse microbiome whose dynamics are important for human health (5, 6). In the context of cellular populations within organisms, the evolution of neoplasms and tumor cells (7–9), interactions within the immune system (10, 11), and the appearance of dominant clones during cell reprogramming (12) exhibit phenomenology akin to ecological competition. Beyond biology (13–15), competitive interactions shape behaviors in a vast array of systems such as competition economics (16) and social networks (17).

A classical example of the effects of interspecies competition—which inspired important ecological competition paradigms—is the differentiation in beak forms of finches in the Galápagos Islands (18, 19). On these islands, dissimilar finch species possess beaks of varying shapes and sizes, allowing them to consume different food sources and thus occupy distinct niches; this type of ecosystem structure is commonly referred to as an ecological niche model (20, 21). Various niche models have been used to describe the community structures observed in diverse ecosystems such as plant grassland communities (22, 23), marine plankton (24), and conservation ecology (25, 26). Commonly, niche specialization results in weaker competition for resources between individuals occupying separate niches (interspecies competition) compared to the competition between individuals of the same kind residing in the same niche (intraspecies competition) (27–29).

Another paradigmatic class of ecological models that are used to describe noisy ecosystems comprises neutral models. In contrast to niche models, in neutral models individuals of all species are considered functionally equivalent, and interactions between them are identical regardless of their species (30–33). One classical example of a neutral model is the Hubbell model, which showed that a neutral process underlying the population dynamics of an ecosystem recovers experimental observations of species abundances in tree communities (31). Subsequently, neutral models have commonly served as the paradigmatic null hypotheses for the exploration of ecological processes in which the differences between interspecific and intraspecific interaction are functionally negligible (30, 34–36). Neutral theories may be viewed as a limit of niche theories where interspecific and intraspecific interactions are equal: In other words, all species reside in completely overlapping niches (21, 37, 38).

In multispecies communities, the intra- and interspecies interactions as well as interactions with the environment can lead to complex community composition and population dynamics of interacting and noisy ecosystems. We address this problem using a minimal ecosystems model that includes factors such as mutations and environmental noise. Our model serves as a minimal null model of noisy competitive ecological systems, against which more complex models can be compared.

Significance

Communities of interacting species are ubiquitous in Nature. Understanding and predicting these communities’ behaviors informs their engineering in important applications in health and ecological conservation. Despite high phenotypic diversity of organisms across ecosystems, observations show commonalities in their community structures. However, it remains incompletely understood how the species interactions and competition shape the population diversity and community structure. Expanding the predictive understanding of interacting and noisy ecosystems beyond commonly employed limited paradigms, we comprehensively investigate the ecological behaviors described by a minimal ecosystems model of interacting species. We find rich behavior with many unexpected regimes. We apply the insights and implications of our model to the range of behaviors observed experimentally in different ecosystems—from bacteria to the immune system.
dynamics; some species survive in the long term, while others are driven to extinction. However, in large communities with high numbers of competing species, it is often impractical or impossible to characterize the entire system composition by the assemblage of abundances for each species. Hence, coarse-grained paradigmatic descriptions are often used to provide general insights into the common behavior of these ecological communities.

Two variables commonly used to characterize complex ecological communities are 1) the richness, reflecting the number of co-occurring species (39, 40), and 2) the species abundance distribution (SAD)—the number of species present at a given abundance. The latter is closely related to the species proportional abundance distribution (SPAD) as well as to the species rank abundance (SRA)—the species ranked in terms of their abundance (33, 41–45). These aggregate variables are observable experimentally and serve as the reporters on the underlying community structure, dynamics, and interaction network (46–49). Richness, for example, is commonly considered to be an indicator of the competition strength and stability of the ecosystem (50–54).

The shape of the SAD is also used as a proxy for the structure of the underlying interactions’ network. For high immigration or weak interspecies competition, the SAD commonly has a peak at high species abundance, away from extinction. This community structure is closely related to the niche models whereby different species coexist: Most species inhabit their own niches with their species abundance fluctuating around the peak of the SAD. Conversely, other ecosystems, such as many microbial communities and T cell repertoires, commonly comprise few high-abundance species alongside highly diverse populations of low-abundance species (43, 55). This unimodal, monotonically decreasing SAD—sometimes called a “hollow-curved distribution”—we refer to as the “rare biosphere” SAD. Interestingly, this behavior is empirically observed in many different ecosystems and is often considered universal (see ref. 56 and references therein). Neutral models have been championed to describe the emergence of this universality, although other theoretical explanations for the rare biosphere SAD in competitive ecosystems have been suggested (44, 57).

Theoretical studies commonly employ a small number of paradigmatic models to quantify the competitive dynamics, the richness, and the abundance distributions in ecological populations. One common model of ecological competition is the deterministic, competitive Lotka–Volterra (LV) model, which has been especially useful in characterizing the niche regime by describing stable species coexistence as stable fixed points of the model. Depending on the ratios of inter- and intraspecies competition strengths, deterministic LV models provide examples of both the “niche-like” regimes of multiple species coexistence and the competitive exclusion where species with weaker intraspecies interactions drive others to extinction (58–61). In complex scenarios, such as when the strengths of interspecific interactions are randomly distributed among different species pairs, multispecies deterministic LV models can exhibit not only deterministic fixed-point coexistence but also chaotic behavior reflected in the SAD shapes and richness (62–66). Beyond disorder in the interaction network, dynamical noise from various sources—both extrinsic and intrinsic—has important effects on the system composition and dynamics, especially in the neutral regime. To capture experimentally observed stochastic fluctuations of population abundances, environmental noise is often introduced into the mathematical models (55, 67–70). In particular, by tuning the strength of environmental noise the shape of the SAD can change from unimodal to bimodal (67), indicating a transition between niche-like and rare biosphere regimes. Incorporating both asymmetric interactions and environmental noise, “patch models” of communities have also been utilized to study coexistence and abundances (71, 72) in island metacommunities.

Regardless of the presence of the external environmental noise or randomness in the interaction network, the demographic noise—the inherent randomness of birth and death events—is ever present and has fundamental impact on the community structure and stochastic population dynamics (31, 33, 73, 74). In particular, demographic noise in neutral systems has been shown to result in an SAD shape characterized by a monotonically decreasing distribution often referred to as a rare biosphere distribution. Consequently, it has been suggested that the rare biosphere SAD observed in many experimental systems is the outcome of neutral dynamics of ecological communities (31, 33, 36, 75). On the other hand, neutral birth–death–immigration processes with demographic noise have also been shown to exhibit bimodal SADs at very low immigration rates (76), breaking from the paradigm wherein neutrality synonymously refers to an SAD of the rare biosphere type. Although demographic noise models have been shown to reproduce the observed features of a number of ecological systems (28, 54, 74, 77), a complete picture of the different regimes of community structures is still missing. In particular, it remains to be fully understood how the interplay of the competition strength, the immigration rate, demographic noise, and the resulting dynamics of species turnover shape transitions between these different community structure regimes.

In this paper, we systematically investigate the full parameter space of the community composition and structure using a competitive LV model with the demographic noise and an interaction network of minimal complexity structure; more complex scenarios may be examined by building on this paradigmatic null model. We show that, beyond the perception of dichotomous neutral-niche regimes, many different regimes of richness and SAD shape emerge from the interplay between the competition strength and immigration in the presence of stochasticity as illustrated in Fig. 1. These regimes exhibit contrasting dynamics that underpin the differences in the community structures in different regimes and the transitions between them.

The paper is structured as follows: In Section 2 we introduce the minimal model. In Section 3 we present our main results, including the regimes boundaries, their richness, and the abundance distributions, as well as their associated underlying dynamics. Finally, in Section 4, we discuss our results in the context of experimental observations.

## 2. Mathematical Models and Methods

The minimal model studied in this paper incorporates three essential features of the ecological processes: competitive interactions, immigration, and intrinsic demographic noise (74, 78). In the model, illustrated in Fig. 1B, the community composition is characterized by the species abundances, \( \bar{n} = (n_1, \ldots, n_i, \ldots, n_S) \), where the discrete random variable \( n_i \) represents the number of individuals of the \( i \)th species, and \( S \) is the total number of species. The dynamics of the system are described by a birth–death process with interactions, whereby the abundance (number of individuals) of any species can increase by one with the birth rate \( q^+ \) or decrease by one with the death rate \( q^- \) defined as

\[
q^+_i(\bar{n}) = r^+ n_i + \mu_i
\]

\[
q^-_i(\bar{n}) = r^- n_i + \frac{r}{\bar{K}} n_i \left( n_i^{-\frac{1}{\bar{K}}} \sum_{j \neq i} \rho_{j,i} n_j \right)
\]

[1]
The death rates include the “bare” per-capita death rate of the organisms that the system possesses no global absorbing extinction state. The per-capita turnover rate is $K$ and the competitive interactions effects that increase the mortality at high population numbers, incorporated through a quadratic term in the death rates. Parameter $\rho_{j,i}$ quantifies the competition strength between species $i$ and $j$; the competition strength (analogous to the niche overlap) remains unexplored. The model illustration. An island with $J$ individuals may migrate from a cloud/mainland, containing $S$ species, into the island with a constant rate $\mu$. This symmetric and homogeneous interaction network has been used in refs. 27, 54, 74, and 77 in contrast to the models wherein the competition strengths are inhomogeneous and drawn from a distribution. This minimal complexity model allows us to investigate the full phase space of the system to examine the underlying principle without extensive and impractical multiparameter sweeps.

The stochastic evolution of the system is described by the master equation

$$
\partial_t \mathcal{P}(\vec{n}; t) = \sum_{i} \left\{ - [q_i^+ (\vec{n}) + q_i^- (\vec{n})] \mathcal{P}(\vec{n}; t) + q_i^+ (\vec{n} - \vec{\epsilon}_i) \mathcal{P}(\vec{n} - \vec{\epsilon}_i; t) + q_i^- (\vec{n} + \vec{\epsilon}_i) \mathcal{P}(\vec{n} + \vec{\epsilon}_i; t) \right\},
$$

where $\vec{\epsilon}_i$ is the standard basis vector and $\mathcal{P}(\vec{n}; t)$ is the joint probability density function for the system to exhibit the species composition $\vec{n}$ at time $t$. In the long-time limit, the system reaches a stationary state where $\partial_t \mathcal{P} = 0$ (SI Appendix, section 2).

The SAD describing the mean fractions of species with $n$ individuals can be related to the marginal single-species probability distribution $P(n)$:

$$
\text{SAD}(n) = \frac{1}{S} \left( \sum_{i=1}^{S} \delta(n_i - n) \right) = \frac{1}{S} \sum_{i=1}^{S} \sum_{n_i=0}^{\infty} \cdots \sum_{n_{i-1}=0}^{\infty} \sum_{n_{i+1}=0}^{\infty} \cdots \sum_{n_{j}=0}^{\infty} \mathcal{P}(\vec{n})|_{n_i=n} = P_i(n) = P(n),
$$

where $\delta$ is the Kronecker delta function, and using the fact that in this homogeneous system the marginal distributions $P_i(n) = P(n)$ of population abundance are identical for all species.

Dynamics of ecological populations can also be described using continuous approximations (SI Appendix and SI Appendix, section 1) (33, 55, 67–70). In particular, in the Fokker–Planck approximation, the continuous deterministic limit of the master equation (Eq. 2), recovers the well-known competitive LV equations

$$
\frac{\partial x_i}{\partial t} = q_i^+ (\vec{x}) - q_i^- (\vec{x}) = rx_i \left( 1 - \frac{x_i}{K} - \sum_{j \neq i} \frac{x_j}{K} \right) + \mu
$$

for the variable $x_i$, which corresponds to the continuous deterministic limit of the discrete variable $n_i$ (84); see SI Appendix, section 1 for further details.

The deterministic steady state is given by

$$
\tilde{x}(S) = \frac{K}{2[1 + \rho(S - 1)]} \left\{ 1 + \sqrt{1 + \frac{4\mu(1 + \rho(S - 1))}{rK}} \right\}.
$$

Note that in the deterministic LV process all species survive with abundance $\tilde{x}$ as long as $\rho \leq 1$ and $\mu > 0$ (28). Conversely, in the stochastic competitive environment the numbers of individuals of each species fluctuate, occasionally reaching extinction. Thus, the number of coexisting species $S^*$ is a stochastic variable as well and may be smaller than the overall number species $S$ in the
immigration flux from the larger basin, with \( S^* \leq S \). The number of coexisting species has a corresponding probability distribution whose evolution is governed by a master equation derived from Eq. 2 (SI Appendix; section 2) (89). The richness, denoted as \( \langle S^* \rangle \), is defined as the average number of the (co)existing species and is related to the SAD via

\[
\langle S^* \rangle = S(1 - P(0)).
\]

Intuitively, this is the sum of the expectation of \( S \) random indicator variables; the richness is determined by \( S \) times the probability that a species is present in the system, \( 1 - P(0) \) (SI Appendix, section 3.A).

No exact analytical solution for the high-dimensional master equation Eq. 2 is known for a general competition strength \( \rho \). To understand the principles of the community organization and the impact of competition, immigration, and demographic noise, we developed approximate analytical solutions to the master equation verified by Gillespie simulations (see SI Appendix, section 2 for details).

### 3. Results

#### A. Mean-Field Approximation

The full master equation Eq. 2 can be reduced to a one-dimensional approximation for the marginal distribution \( P(n) \) with effective birth–death rates (SI Appendix, section 2.A). The SAD, \( P(n) \), is obtained as a self-consistent stationary solution of this equation as

\[
P(n) = P(0) \frac{(r^+)^n(\mu/r^+)^n}{n! \prod_{i=1}^{n} \left( 1 + r^+ - r \frac{n_i}{K} + \rho \sum_{j \neq i} S_{j, i} n_i / K \right)}.
\]

To obtain an analytical approximation to \( P(n) \) we use a mean-field closure for the unknown conditional averages \( \langle n_j | n_i \rangle \) instead of \( \sum_{j \neq i} S_{j, i} n_j / n_i \), which can be solved numerically. We have found a good agreement between exact stochastic simulation results and this mean-field approximation for most of the parameter space examined.

Following Eq. 6, the average richness in the mean-field approximation is

\[
\langle S^* \rangle = S \left( 1 - \frac{1}{1 \tilde{F}_1[a, b + 1; c]} \right),
\]

where \( P(0) = 1/1 \tilde{F}_1[a, b + 1; c] \) is the normalization constant of \( P(n) \) where \( \tilde{F}_1[a, b; c] \) is the hypergeometric Kummer confluent function, with \( a = \mu / r^+ \), \( b = r^+ - K + r \rho (S - 1) \langle n \rangle / r \), and \( c = r^+ K / r \). The exact solution for the distribution of the number of coexisting species, \( S^* \), can be obtained for \( \rho = 0 \) (a binomial distribution) and \( \rho = 1 \) (a sum of hypergeometric functions) (SI Appendix; section 3) (74). For intermediate competition strengths, \( 0 < \rho < 1 \), a mean-field approximation results in a binomial distribution for the species richness distribution as in ref. 89; however, we discuss how this mean-field solution differs from the richness distribution from simulations in SI Appendix, section 3.

#### B. The System Exhibits Rich Behavior with Distinct Regimes of Population Structures Controlled by Competition Strength, Immigration Rate, and the Species Number

Depending on the values of the competition strength and the immigration rate, the number of species, and the system size, the population can exhibit a number of different regimes of behavior that can be categorized by their richness and the shape of their SAD, as visualized in Fig. 2 and described below.

##### B.1. Richness regimes

In the classical deterministic LV model, the systems exhibits either an interior fixed point with full coexistence of all species at abundances given by Eq. 5 or mass extinction with a single surviving species, in agreement with the well-known Gauss’s law of deterministic competitive exclusion (28). By contrast, the stochastic model may exhibit partial coexistence due to the temporary extinctions of some species driven by the abundance fluctuations arising from the demographic noise. Overall, the number of coexisting species and their abundances are determined by the balance between the immigration and the competition-induced stochastic extinction events. Three distinct richness regimes can be discerned as shown in Fig. 2, based on the variations of the richness of the system \( \langle S^* \rangle \) in different regions of the \( (\rho, \mu, S) \) parameter space.

At low competition strength—region a in Fig. 2A—all species coexist so that the richness of the system is equal to the total number of species \( \langle S^* \rangle \approx S \), similar to the deterministic regime. In this regime, each species effectively inhabits its own niche because the interspecies competition is not sufficiently strong to drive any of the species to extinction in the presence of abundance fluctuations arising from the demographic noise. The probability for a species to be present is determined by the balance of its immigration and the extinction rate. At higher immigration rates this regime extends into regions with higher competition strength \( \rho \); high immigration rates stabilize full richness populations even with a relatively high competition strength.

In the second regime—region b in Fig. 2A—only a fraction of the species are simultaneously present on average, which we denote as the partial coexistence regime. In this regime, the immigration influx is not high enough to prevent temporary stochastic extinctions of some species resulting from the competition.

At very high competition strengths a complete exclusion regime—region c in Fig. 2A—is found. High competition along with the very low immigration rates act in unison to reduce the richness to below two species on average. Although regime c may appear similar to regime b since both present partial coexistence, they are distinguished by key behaviors as explained below.

Note that the stochasticity is central to the effect of the competition on the observed richness. Stochastic fluctuations increase the risk of extinction with increasing competition strength, unlike in the deterministic case where the richness is independent of the competition strength for \( \rho < 1 \) (28).

##### B.2. SAD shape and modality regimes

Besides determining the richness, the balance between immigration and stochastic competitive extinctions also dictates the mean abundances of the individual species and the SAD. When the immigration influx of individuals into the system is higher than the average outflux due to the transient extinctions, shown in Fig. 2B as region I, most species are forced away from extinction. In this regime, the SAD is unimodal with a peak at relatively high species abundances \( \tilde{n} \) approximately located at

\[
\tilde{n} = \frac{K - \rho(S - 1)\langle n \rangle}{2} \left( 1 \pm \sqrt{1 + 4 \frac{(\mu - r^+)K}{r(K - \rho(S - 1)\langle n \rangle)^2}} \right).
\]
which agrees with the simulation results, as shown in Fig. 3 (SI Appendix, section 2.B).

At lower immigration rates—regime II in Fig. 2B—the immigration rate is insufficiently strong to overcome the competition-driven temporary extinctions of some species, and the SAD develops an additional peak around \( n = 0 \) corresponding to the temporarily extinct species. The subset of the “quasi-stable” coexisting species dominates the population number with abundances that fluctuate around the niche-like abundance peak, \( \tilde{n} \). Their persistence at dominant abundances is punctuated by rare fluctuation-driven extinctions and the occasional invasion of a temporarily extinct species into the dominant population. By contrast, the dynamics of species in the \( n = 0 \) zero peak are characterized by the rapid turnover of the remaining species close to extinction. This balance between the immigration and the stochastic competitive extinctions may be related to the tradeoffs in competitive ability and dispersal (immigration) in metacommunity population dynamics (72, 90).

At low immigration rates, the peak at Eq. 9 coincides with the deterministic stable solution in Eq. 5 (SI Appendix, section 4.B):

\[
\lim_{\mu \to 0} \tilde{n} = \lim_{\mu \to 0} \tilde{x} \left( \langle S^* \rangle \right) = \frac{K}{1 + \rho \left( \langle S^* \rangle - 1 \right)}. \tag{10}
\]

Namely, in the bimodal regime the coexisting dominant species are fluctuating around \( \tilde{n} \), which, at low immigration, is the deterministic fixed point with \( \langle S^* \rangle \) species. In this regime, the dynamics of the fluctuations of the abundant species around \( \tilde{n} \) can be heuristically understood as a spatially dependent diffusion in an effective potential well of the Fokker–Planck equation (Section 2 and SI Appendix, section 1).

Somewhat unexpectedly, at low immigration rate \( \mu < 0.05 \), the bimodal regime extends onto the neutral line at \( \rho = 1 \) where the SAD has been commonly believed to have the monotonically decreasing rare biosphere shape (31, 75). Surprisingly, in this regime the competition is so strong that most of the time either no species is present at high abundance or only one species survives in a kinetically “frozen” and long-lived quasi-stable state with an abundance \( \tilde{n} \approx K \), as observed previously (76); this is region IIc in Fig. 2C.

Furthermore, at the intermediate immigration rates and relatively high competition strengths we observe a unimodal behavior with a peak at zero rather than at a finite \( \tilde{n} \) —regime III in Fig. 2B. In this regime, the competition is strong enough so that the fluctuations competitively drive species to temporary extinction before any of them are able to establish a quasi-stable state at a high abundance. All species undergo rapid turnover around zero, resulting from the balance between random immigration and extinction events. This regime corresponds to what was previously described as the rare biosphere: Fewer numbers of species are found at higher abundances, resulting in a monotonically decreasing SAD. This SAD shape is classically recognized as a hallmark of a rare biosphere regime. However, as shown in Fig. 2 the unimodal regime III unexpectedly extends substantially beyond the neutral manifold \( \rho = 1 \), into the nonneutral regions with \( \rho < 1 \), and the monotonically-decreasing SAD persists even for
These two peaks are visibly separated only when the richness is low and carrying capacity is high, since solutions of Eq. 10 for different $S^*$ are more distant in this regime.

The transitions between the different modality regimes and the corresponding changes in the SAD shapes are illustrated in Fig. 3. Generally, at low competition strength $\rho$ the species are practically independent of each other, residing in largely nonoverlapping niches and with their typical abundance $\tilde{n}$ close to the carrying capacity $K$. Increasing competition strength $\rho$ makes it harder to sustain the coexisting species at high abundances, and accordingly $\tilde{n}$ decreases, as illustrated in Fig. 3 A, Top and Fig. 3B. With further increase in $\rho$ the system behavior bifurcates, depending on the immigration rate $\mu$. At high immigration rates, $\mu \gtrsim 0.05$, the competition-driven decrease in $\tilde{n}$ continues up to the critical competition strength (calculated in the next section) where the peak around $\tilde{n}$ disappears (Fig. 3 A, Top Right), as the system is not able to sustain quasi-stable niche-like species coexistence. This corresponds to the transition from the bimodal region II to the rare biosphere region III in Fig. 2. At lower immigration rates (Fig. 3 A, Top Left), further increases in the competition strength eventually cause mass species extinctions that allow the remaining few dominant species to maintain higher abundances (region III in Fig. 2). As $\rho \to 1$, the system transitions to the region IIC of Fig. 2: only one dominant species remains, as described in ref. 76, with abundance fluctuating around $K$.

**B.3. Global phase diagram and regime boundaries.** In this section we describe the complete phase diagram of the system defined by the intersection of the different richness and the SAD shape/modality regimes, derive the regime boundaries, and discuss the transitions between them, as shown in the $(\mu, \rho)$ space in Fig. 2C and in $(S, \rho)$ space in Fig. 2D. We show that the boundaries between different regimes observed in simulations can be understood within simple mean-field theories and discuss the underlying physical factors responsible for the transitions between different regimes.

We define the boundary between the full coexistence (a) and partial coexistence (b) regimes to be at $(S^*) = S - 1/2$: the midpoint between full richness $S^* = S$ and the loss of one species on average. Similarly, the boundary between the partial coexistence (b) and exclusion (c) regimes is located at $(S^*) = 3/2$, that is to say where the richness is between one and two species such that on average only one species is present in regime c.

To derive the boundaries corresponding to the transitions of the SAD modality regimes, we use discrete derivatives of the approximated SAD to determine the existence of peaks and their location (SI Appendix, section 4.C). The immigration-dominated regime I is characterized by a unimodal SAD with a peak at the positive root of $\tilde{n}$ given in Eq. 9. Compared to this immigration-dominated regime, the neighboring bimodal and monotonically decreasing unimodal regimes—regions II and III, respectively—differ by the emergence of a new mode at zero abundance.

Thus, the boundary that defines transitions to either regime II or III from the immigration-dominated regime I is described by a flattening of SAD at $n = 0$: $\partial P(\tilde{n})/\partial |\tilde{n}|_{\tilde{n}=0} = 0$. In the discrete case, this heuristically corresponds to $P(0) = P(1)$. Combining this condition for the boundary with the global balance of the master equation Eq. 2 results in the rate balance equation, $(q^+_{\tilde{n}}(\tilde{n})|_{\tilde{n}=0}) = (q^-_{\tilde{n}}(\tilde{n})|_{\tilde{n}=1})$.

In the mean-field approximation, this boundary is found at

$$
\mu = r^- + \frac{r^+}{K[1 + \rho(S - 1)]}.
$$

[11]

This equation recovers the similar transition for $\rho = 1$ derived independently in ref. 76.
The boundary between the bimodal regime II and the rare biosphere regime III is characterized by the disappearance of the peak at high abundance \( n \) in Eq. 9. In the bimodal regime at least one solution to \( n \) is real and positive; as such a maximal, real peak exists. Conversely, in the rare biosphere regime, both solutions of \( n \) are negative or imaginary. We find that the boundary between the real and imaginary \( n \) is

\[
 r(K - \rho(S - 1)\langle n \rangle)^2 = 4(r^+ - \mu)K \tag{12}
\]

and the transition line between positive and negative solutions, \( \tilde{n} = 0 \), is

\[
 \frac{(K - \rho(S - 1)\langle n \rangle)^4}{16} = 1 + \frac{K(\mu - r^+)}{r}. \tag{13}
\]

The intersection of these two conditions defines the rare biosphere regime and is shown as the blue line in Fig. 2B and C.

The modality and the richness of the system are also affected by the number of species \( S \) as shown in Fig. 2D. In brief, the frequency of the immigration events rises as more species are present in the immigration flux. Increased immigration causes the total population to rise without providing more room for each species in the system; this increases the stochastic competition, driving more species to extinction. Hence, as \( S \) increases, the transition from the bimodal regime II to the unimodal regime III occurs at lower values of competition strength \( \rho \), and the fraction of the concurrently surviving species decreases. This effect has been qualitatively observed experimentally (92), and we return to it in Section 4.

These analytical expressions for the regime boundaries—confirmed by stochastic simulations—provide insights into the effects of different control parameters on the regime boundaries. In particular, using the low \( \mu \) deterministic approximation for \( \langle n \rangle \approx K/[1 + \rho(S - 1)] \) shows that the location of the boundary of the rare biosphere regime grows proportionally to the carrying capacity and is a decreasing function of the number of species \( S \). Thus, the size of the rare biosphere regime increases with the number of species \( S \) as shown in Fig. 2D, whereas increasing the carrying capacity shrinks this regime (SI Appendix, section 5).

C. Kinetics of the Species Turnover, Extinction, and Recovery Underlie the Transitions between Different Regimes. To better understand the driving forces for the transitions between the different regimes, we focused on the underlying kinetics of species turnover and fluctuations. There is a stark contrast in the kinetics of an individual species in the unimodal rare biosphere regime III and the niche-like regimes with a peak in SAD at nonzero abundance, as shown in Fig. 4A. In regime III, all species undergo rapid turnover in the relatively broad range of abundances around extinction. By contrast, in regimes I, II, and IV the quasi-stable dominant species undergo fast fluctuations around the coexistence peak at \( \tilde{n} \) in addition to fast turnover of the remaining species near extinction. These fluctuations around the quasi-stable abundance are punctuated by the temporary extinctions and the reverse invasions of temporarily extinct species into the dominant niche-like peak.

To characterize the kinetics in different regimes, we calculate the mean first-passage times (MFPT) \( T(a \to b) \) of the transitions between different abundance levels (a and b), using the one-dimensional backward master equation (SI Appendix, section 6) (93, 94).

We first focus on the ratio of the MFPT of the transition from dominance to exclusion to the MFPT of return to the dominant abundance level (starting from the dominant abundance level), \( T(\tilde{x}((S^*)) \to 0)/T(\tilde{x}((S^*)) \to \tilde{x}((S^*))) \), shown in Fig. 4B.
Here, $\tilde{x}$, given in Eq. 5, is the deterministic extension of the peak abundance $\tilde{n}$ in regimes without a nonzero abundance peak. Large values of this ratio signify that the extinction rate from $\tilde{x}(\langle S^* \rangle)$ is much slower than the rate of local fluctuations in the effective potential well around $\tilde{x}(\langle S^* \rangle)$. Accordingly, Fig. 4B shows that this ratio is high in the bimodal and immigration-dominated regimes. Conversely, this ratio is lower within the rare biosphere regime that does not possess a high abundance peak with quasi-stable coexisting species. As shown in Fig. 4B, this ratio approximately delineates the rare biosphere regime from the niche-like regimes and its contour lines qualitatively recover the boundaries of region IIb in Fig. 2C; see SI Appendix, section 6 for further discussion.

The second ratio, which underlies the richness transitions in the system, $T(0 \to \tilde{x}(\langle S^* \rangle))/T(0 \to 0)$ (Fig. 4C), relates the MFPT from extinction at zero abundance to dominance at $\tilde{x}$ to the mean return time to extinction. This ratio gives a rough measure of the number of species present in the system: $T(0 \to 0)$ is inversely proportional to $P(0)$ and $T(0 \to \tilde{x}(\langle S^* \rangle))$ is heuristically inversely proportional to the number of coexisting species (SI Appendix, sections 3A and 6). As such, this MFPT ratio approximates the ratio of the average number of temporarily extinct species, $S - \langle S^* \rangle$, to the average number of existing species, $\langle S^* \rangle$ (Fig. 4C). As shown in Fig. 4C the ratio qualitatively recovers the boundaries of richness regimes in Fig. 2 in most regions of the parameter space.

These MFPTs not only serve to interpret the underlying dynamics that give rise to different regimes; they may also be more easily experimentally measured than steady-state distributions. Further discussion on the dynamical features is presented in SI Appendix, section 6.

4. Discussion

Ecological systems display a wide variety of different behavior regimes that have been commonly analyzed through a limited number of paradigmatic models such as the “niche” and “neutral” theories. However, it remains incompletely understood what features of ecological population structure and dynamics are universal and which ones are system specific, how different models relate to each other, and what behavior is expected in the full range of the parameter space. Using a minimal model of the competitive population dynamics with demographic noise, we have investigated the different regimes of the population structures and dynamics as a function of the immigration rate $\mu$ and the competition strength $\rho$, as well as the number of species $S$. Although this minimal model may not fully capture the more complex interaction structures of many ecological communities, it exhibits rich and unexpected behaviors paralleling many experimental observations (Table 1) and illuminates the underlying mechanisms that shape population structures in different ecosystems.

We have focused on the system richness reflecting the number of the coexisting species and the SAD shape as the characteristics of the different population regimes, using a combination of simulations and analytical mean-field approaches. Our analysis shows that the ecosystem behaviors can be partitioned into different regimes of richness and SAD shape/modality, parameterized by the immigration rate and the competition strength—which is analogous to the competitive overlap discussed in other studies and references therein (27, 77).

Our model recovers the limits of the well-known rare biosphere and the niche-like regimes. In particular, at $\rho = 1$ and intermediate values of $\mu$, the SAD has the monotonically decreasing shape characteristic of the classical neutral regime. On the other hand, at low competition strength, the system SAD exhibits a peak at high species abundance where all species coexist. We recover the expected regime where different species effectively occupy distinct ecological niches. Notably, even independent species with no interspecies competition with $\rho = 0$ may present either a unimodal or a bimodal SAD depending on the immigration rate, as shown in Fig. 2 B and C. Unlike the immigration-dominated high-abundance peak at high immigration rates, at the very low immigration rates the SAD is peaked around zero due to high extinction probability solely from the intraspecies competition.

We found that, contrary to the common expectation that different species inhabit separate niches away from neutrality, the system can maintain the monotonically decaying rare biosphere SAD even at low competition strength (up to $\rho \approx 0.1$) as shown in regime III in Fig. 2. Similarly, unexpectedly, at the very low immigration rates, the system SAD maintains the peak at nonzero abundance characteristic of niche-like regimes even for the high values of the competition strength $\rho$ usually considered to be in the rare biosphere domain (regime IIc) in Fig. 2 and Section 3B.

We have also uncovered an unusual—and to the best of our knowledge hitherto not described—regime characterized by the multimodal SAD with more than one positive, quasi-stable abundance peak (regime IV in Fig. 2). This multimodality arises from the richness fluctuations in this regime: The number of coexisting species is switching randomly between two relatively long-lasting states with $S^* = 1$ and $S^* = 2$. Thus, one peak of the SAD is found around $\sim K$ and the other one in the vicinity of $\sim K/2$, as explained in Section 3B. We observe that for low $K$, the multimodal regime is nonexistent and appears as $K$ increases; see the corresponding phase diagrams in SI Appendix, section 5.

Transitions of the SAD between different regimes occur through different routes. In particular, as the immigration rate increases, the SAD peak of the bimodal regime II at $\rho = 1$ gradually decreases in height without significantly shifting its location until it disappears at the boundary of the rare biosphere regime III. By contrast, at lower competition strengths $\rho < 1$, the transition from the bimodality to the rare biosphere regime occurs via simultaneous changes in the peak’s height and location. This is discussed in Section 3B.

Table 1. Qualitative classification of observed population regimes in various ecological systems

| System (ref.)                | Regimes                                           | Observations                                      |
|------------------------------|---------------------------------------------------|---------------------------------------------------|
| Microbial competition (92)   | Stable full coexistence (IIa), stable partial coexistence (IIb), persistent fluctuation (IIIb) | Community composition/richness/ fluctuating communities                     |
| Global bird species (106)    | Unimodal-log skew (I)                             | SAD                                               |
| Plankton (107)               | Power-law decay (III)                             | SAD and SRA                                       |
| Coral (102)                  | Multimodal (IV)                                  | SAD                                               |
| Arthropods (108)             | Multimodal (IV)                                  | SAD                                               |
| T cell receptors (109)       | Bimodal (II) and unimodal (III)                   | SRA and time series                               |
| Microbial competition (110)  | Rare biosphere (III) and niche-like (I and II)    | SRA and operational taxonomic units (OTUs)         |
| Gastrointestinal microbiomes (101) | Rare biosphere (III)                             |                                                   |
We show that the population structures in different regimes and the transitions between them stem from the underlying dynamics of species fluctuations, extinctions, and invasions. In the rare biosphere regimes, all species undergo relatively fast turnover around extinction. This is reflected in the low ratio of the turnover to the extinction mean first-passage times. Conversely, in the niche-like regimes the system develops two additional timescales: relatively fast fluctuations about the high abundance peak and the long waiting times for the transitions from the quasi-stable coexistence at high abundance to extinction. This is reflected in the fact that the ratio of the mean extinction time to the mean time of return to dominance is higher in the niche-like regime, as discussed in Section 3.C.

Interestingly, ecological regimes akin to those predicted by our demographic noise model (except for the multimodal SAD regime) have been also found using deterministic, noiseless LV models with a random matrix of interspecies competitive competition strengths (64, 83, 92, 95, 96). However, the underlying mechanisms that give rise to the apparently similar regimes in the two model types are very different. In the demographic noise model, the partial richness niche-like regime (IIb) (Fig. 2C) comprises the quasi-stable coexistence of a subset of species at a positive abundance in parallel with the temporary stochastic extinctions of other species. By contrast, in the deterministic LV models with random asymmetric interactions, the partial richness niche-like regime comprises a large number of saddle fixed points where different sets of species are competitively excluded deterministically. At higher competition strengths, the deterministic system transitions to the chaotic behavior that resembles the rare biosphere regime (III) (Fig. 2C); however, the nature of the species turnover and the shape of the SAD are different from the results we presented in Section 3 (64, 92, 97).

The existence of the predicted regimes and the transitions between them can be tested experimentally by measuring the SAD and the dynamics of the species abundances in ecosystems with varying immigration and competition strengths, numbers of species, and effective carrying capacities. Measurements of the SADs and the community compositions have become more attainable due to the advances in single-cell gene-sequencing techniques (1, 12, 92), overcoming the difficulties of SAD estimation due to data limitations. Long-term observations may provide measurements of the stationary species abundance distributions (98). Although it may be difficult to experimentally determine and control the immigration rate, the competition strength, and the carrying capacity, practical proxies for these parameters exist. By way of an example, the flow rate carrying bacteria into a chamber of a microfluidic device is a well-controlled quantity that approximates well the immigration rate for populations encased in the chamber (99). Another commonly used and robustly estimated experimental observable is the SRA, which can be used to infer the SAD to which it is closely mathematically related (SI Appendix, section 7), although in practice the conversion might be constrained by limitations of noise and quantity of the experimental data.

The asymptotic behavior of the SADs may show qualitative dissimilarities between distributions, allowing one to discern different regimes of behavior among the experimental observations. In the mean-field approximation, the asymptotic behavior of the model’s SAD on the neutral line $\rho = 1$ is well approximated by a power law with an exponential cutoff (SI Appendix, section 2.C). This asymptotic is similar in functional form to the SADs commonly found by Hubbell models of a neutral birth–death process with a fixed total population size (36, 75). Notably, the Yule process that is often used to model neutral processes also results in the SAD of a similar form. However, the Yule process is substantially different from the model of this paper because it does not include interspecies interactions and reaches the steady-state SAD only if the effective death rate is higher than the effective birth/immigration rate (100).

In Table 1, we qualitatively compare the family of the regimes predicted by our model to the various behaviors inferred from experimental findings based on the SAD measurements and population abundance time series. The apparent abundance of the neutral ecosystems observed experimentally—such as gastrointestinal microbiomes—may pertain to our finding (Section 3.B) that the rare biosphere regime extends substantially beyond the neutral line $\rho = 1$: Nonneutral communities may appear neutral as they exhibit the SAD’s characteristic of neutral communities (101). Furthermore, multimodal SADs predicted by our model that are related to the richness fluctuations may provide an explanation for the multimodal SADs observed in some ecological data, complementary to the existing explanations such as spatial heterogeneity or emergent neutrality (63, 102).

One quantity that is relatively easy to control experimentally is the total number of species $S$. The regimes predicted by the model and the transitions between them are shown in Fig. 2D: Our model yields rare biosphere regimes for high $S$ and $\rho$, which are characterized by high-turnover dynamics, and niche-like regimes with more stable behavior at lower $S$ or $\rho$. These predictions qualitatively agree with the experimentally observed phase space in ref. 92, which were previously explained within the deterministic LV models with a random interaction matrix (92). The fact that both the deterministic LV model with a random interaction matrix and the homogeneous LV model with demographic noise are in qualitative agreement with the experimental data raises interesting and important questions concerning the interplay of stochastic and deterministic dynamics in determining the community composition.

Another quantity that may enable qualitative and quantitative testing of different models is the carrying capacity $K$, which may be controlled experimentally in some systems. As shown in SI Appendix, Section 5, the rare biosphere regime shrinks in size with increasing $K$ because a higher carrying capacity can sustain higher average abundance, and larger (less likely) fluctuations are needed for the extinction events to occur. Higher average abundance together with insufficiently strong fluctuations result in longer MFPTs from dominance to extinction abundances and vice versa. These effects will be investigated in future work.

In the context of other ecological theories, the competition strength, as defined in this work, can be viewed as a quantification of the heuristic notion of the niche overlap, and we observe that decreasing niche overlap results in richness increases as suggested previously (103, 104). Our model also serves as a quantitative example of some of the coexistence-promoting mechanisms of the contemporary ecological theory; we explore stabilizing mechanisms that increase richness via decreases in niche overlap, such as fluctuation-dependent processes and fitness–density covariance (29, 105). In particular, the demographic noise model studied here exhibits fluctuation-dependent mechanisms that promote richness as species are able to coexist at high abundance in our model.

We expect that the minimal model of this paper can be used for more complicated scenarios, including more complex distributions of the interaction network $\rho_{i,j}$, speciation to probe the interaction of the natural selection, and interspecies interactions and population diversity and structure.

Finally, our model of a local island community in the mainland–island ecosystem (Fig. 1) can be expanded to many-island models or many-patch dynamics (71, 72). These many-island and many-patch models examine the interplay
between competition and dispersal rate (72) and its effects on the diversity of the metacommunity, a prominent topic in community ecology and the study of the human microbe. The patch models may address how coexistence and persistence are influenced by spatial heterogeneity and environmental noise in a demographic noise formulation. Future work will explore integration of our model into other scenarios to predict species fitness, nonequilibrium coexistence, and their connection to broader qualitative ideas in ecology.

Materials and Methods

The solution for the master equation Eq. 1 is simulated using the Gillespie algorithm with 10^8 time steps. We use r = 2, r = 1 = 100. Modalities' classification is numerically executed after smoothing the simulated SAD. The MFPF is evaluated via the simulated SAD [x(S^*) is rounded], where a unidimensional approximation of the process is considered; see details in SI Appendix, section 6.

Data, Materials, and Software Availability. The code to run the simulations and analysis of the multispecies data is available on GitHub (https://github.com/jbRothschild/project-abundance/tree/PNAS)(111). 

ACKNOWLEDGMENTS. We acknowledge helpful discussions and comments from all the members of the Goyal and Zillman groups. A.Z. acknowledges the support from the National Science and Engineering Research Council of Canada (NSERC) through the Discovery Grant Program RGPIN-2022-04909. S.G. acknowledges the support from the NSERC through the Discovery Grant Program and from the Medicine by Design Program at the University of Toronto.
68. W. Verheert, Explaining general patterns in species abundance and distributions. Nat. Educ. Knowl. 3, 38 (2011).
69. M. S. Fowler, L. Rukolaainen, Colonization, covariance and colour: Environmental and ecological drivers of diversity-stability relationships. J. Theor. Biol. 324, 32–41 (2013).
70. G. Barabási, M. J. Michalka-Smith, S. Allesina, The effect of intra- and interspecific competition on coexistence in multispecies ecosystems. Am. Nat. 188, E1–E12 (2016).
71. S. N. Evans, P. L. Ralph, S. J. Schreiber, A. Sen, Stochastic population growth in spatially heterogeneous environments. J. Math. Biol. 66, 423–476 (2013).
72. M. Tejero, C. Quiñinao, R. Rebolloledo, P. A. Marquet, Coexistence, dispersal and spatial structure in metacommunities: A stochastic model approach. Theor. Ecol. 14, 279–302 (2021).
73. D. Alonso, P. S. Elosee, A. J. McKane, The merits of neutral theory. Trends Ecol. Evol. 21, 451–457 (2006).
74. B. Haegeeman, M. Luqueau, A mathematical synthesis of niche and neutral theories in community ecology. J. Theor. Biol. 269, 150–165 (2011).
75. G. J. Baxter, R. A. Blythe, A. J. McKane, Exact solution of the multi-allelic diffusion model. Math. Biosci. 209, 124–170 (2007).
76. S. Xu, T. Chou, Immigration-induced phase transition in a regulated multispecies birth-death process. J. Phys. A Math. Theor. 51, 425602 (2018).
77. J. A. Captain, S. Cuenda, D. Alonso, Competitive dominance in plant communities: Modeling approaches and theoretical predictions. J. Theor. Biol. 502, 1,10349 (2020).
78. A. J. Black, A. J. McKane, Stochastic formulation of ecological models and their applications. Trends Ecol. Evol. 27, 337–345 (2012).
79. P. Chesson, Updates on mechanism of maintenance of species diversity. J. Ecol. 106, 1773-1794 (2018).
80. R. M. MacArthur, Species packing and competitive equilibrium for many species. Theor. Popul. Biol. 1, 1–11 (1970).
81. P. Chesson, MacArthur’s consumer-resource model. Theor. Popul. Biol. 37, 26–38 (1990).
82. J. P. O’Dwyer, Whence Lotka-Volterra? Theor. Popul. Biol. 61, 441–452 (2008).
83. S. Allesina, S. Tang, Stability criteria for complex ecosystems. Nature 483, 205–208 (2012).
84. C. W. Gardner et al., Handbook of Stochastic Methods (Springer, Berlin, Germany, 1985), vol. 3.
85. G. Grimmett, D. Stirzaker, Probability and Random Processes (Oxford University Press, 2001).
86. J. Schnakenberg, Network theory of microscopic and macroscopic behavior of stochastic reaction networks. Adv. Appl. Probab. 25, 518–548 (1993).
87. A. Gupte, C. Brit, M. Khakhmash, A scalable computational framework for establishing long-term behavior of stochastic reaction networks. PLOS Comput. Biol. 10, e1003669 (2014).
88. P. A. Marquet, M. Tejero, R. Rebolloledo, “What is the species richness distribution?” in Unresolved Problems in Ecology, A. Dobson, R. D. Holt, D. Tilman, Eds. (Princeton University Press, 2020), pp. 177–188.
89. R. H. MacArthur, E. O. Wilson, The Theory of Island Biogeography (Princeton University Press, 1967).
90. S. Goyal, S. Kim, I. S. Chen, T. Chou, Mechanisms of blood homeostasis: Lineage tracking and a neutral model of cell populations in thymus macaques. BMC Biol. 13, 85 (2015).
91. J. Hu, D. R. Amor, M. Barbier, G. Bunin, J. Gore, Emergent phases of ecological diversity and dynamics mapped in microcosms. bioRxiv [Preprint] (2021).
https://doi.org/10.1016/j.mce.2021.10.28.64639. Accessed 1 March 2022.
92. S. Iyer-Biswas, A. Zilman, Continuous-time processes. Oikos 1243–1249 (2018).
93. E. G. Landman, A. A. Misbah, A new approach to the analysis of fluctuation phenomena. J. Phys. A Math. Theor. 48, 1008–1016 (2008).
94. T. Oakes, The importance of sampling strategies in ecological research. Am. Nat. 177, 258 (2010).
95. R. M. May, Will a large complex system be stable? Nature 238, 413–414 (1972).
96. S. Allesina, M. Pascual, Network structure, predator-prey modules, and stability in large food webs. Theor. Ecol. 1, 55–64 (2008).
97. G. Bunin, Ecological communities with Lotka-Volterra dynamics. Phys. Rev. E 95, 042414 (2017).
98. W. J. Siefert, The basic processes of microbial community dynamics. J. Theor. Biol. 324, 124–170 (2013).
99. J. HilleRisLambers et al., Rethinking community assembly through the lens of coexistence theory. Annu. Rev. Ecol. Evol. Syst. 43, 109–122 (2012).
100. T. J. Matthews, P. A. Borge, R. J. Whitaker, Multimodal species abundance distributions: A deconstruction approach reveals the processes behind the pattern. Oikos 123, 533–544 (2014).
101. J. Rothchild, project-abundance. GitHub. https://github.com/jbRothschild/project-abundance/tree/PNAS. Deposited 3 October 2022.