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## LETTER

# A general framework for species-abundance distributions: Linking traits and dispersal to explain commonness and rarity

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## Abstract

Species-abundance distributions (SADs) describe the spectrum of commonness and rarity in a community. Beyond the universal observation that most species are rare and only a few common, more-precise description of SAD shape is controversial. Furthermore, the mechanisms behind SADs and how they vary along environmental gradients remain unresolved. We lack a general, non-neutral theory of SADs. Here, we develop a trait-based framework, focusing on a local community coupled to the region by dispersal. The balance of immigration and exclusion determines abundances, which vary over orders-of-magnitude. The local trait-abundance distribution (TAD) reflects a transformation of the regional TAD. The left-tail of the SAD depends on scaling exponents of the exclusion function and the regional species pool. More-complex local dynamics can lead to multimodal TADs and SADs. Connecting SADs with trait-based ecological theory provides a way to generate more-testable hypotheses on the controls over commonness and rarity in communities.

## KEYWORDS

competition, mass effects, metacommunity, species-abundance distributions, trait-abundance distributions, trait-based model

## INTRODUCTION

Species-abundance distributions (SADs) describe the distribution of population densities of all the species in a community. They are intermediate-complexity descriptors of the diversity of a community: more informative than species richness but less detailed than a list of species and their abundances (McGill et al., 2007). Over almost a century, ecologists have collected countless

SADs from natural communities. The universally observed pattern is that most species in a community are rare, while a few are common, with abundances ranging over orders of magnitude (McGill et al., 2007). Further generalities about the shape of SADs remain controversial (Ulrich et al., 2010), as do the mechanisms behind them. Common species drive ecosystem functioning (Grime, 1998; Winfree et al., 2015), but rare species can provide adaptive capacity in changing environments

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(Norberg et al., 2001; Yachi & Loreau, 1999), while facing a higher risk of extinction (Terborgh & Winter, 1980). To understand the mechanisms behind SADS is to understand how communities are structured, which is essential to predict how they will reorganise under anthropogenic environmental change.

McGill et al. (2007) categorised 27 theoretical models of SADS, including purely statistical models (log-series, Fisher et al., 1943; log-normal, Preston, 1948), niche-apportionment models (geometric, Motomura, 1932; broken stick, MacArthur, 1960, Tokeshi, 1990) and single-species models (Engen & Lande, 1996a, 1996b). However, only mechanistic models based on multispecies population dynamics can simultaneously generate predictions about how species' abundances relate to their traits, how community structure changes along environmental gradients, and how communities will reorganise under environmental change, so we focus on them.

Vellend (2010) identified four key processes that shape communities: selection (niche and fitness differences), ecological drift (demographic stochasticity), speciation and dispersal. Hubbell's neutral theory (2001) combines ecological drift, speciation and dispersal but lacks selection. It generates realistic SADS, but its central assumption that species are identical contradicts patterns found in nature (Harpole & Tilman, 2006). However, with some notable exceptions (Engen & Lande, 1996a, 1996b; Wilson et al., 2003), most purely niche-based models fail to generate realistic SADS: it can be difficult to get more than a few species to coexist (Edwards et al., 2018), and when they do, they typically have comparable abundances. It seems unlikely that purely niche-based models can recreate the orders-of-magnitude variation observed in species abundances without carefully tuned parameters.

One solution to this conundrum is to incorporate processes acting at broader spatial or temporal scales into our explanations of local community structure. Spatial and temporal heterogeneity provide powerful mechanisms of species coexistence (Chesson, 2000; Mouquet & Loreau, 2003). Immigration to a local community can occur in space, from other communities in the region (regional species pool, assumed to be fixed), or in time, from a reservoir of resting stages (Lennon & Jones, 2011). The addition of immigration to niche-based models trivially solves the problem of the local co-occurrence of many species (Chesson, 2000; Loreau & Mouquet, 1999; Shmida & Ellner, 1984), but as we will show, naturally results in order-of-magnitude variation in population density. Empirical studies have shown that such 'mass effects' can play an important role in maintaining local diversity (Shmida & Wilson, 1985).

While simulations of particular models have shown that combining immigration from a regional species pool with local interactions results in realistic SADS (Hughes, 1986; Mouquet & Loreau, 2003; Vergnon et al., 2012; Wilson & Lundberg, 2004), these models are

not amenable to analytical treatment and hard to generalise. Therefore, a general theoretical framework that merges regional and local, niche-based processes to explain SADS is lacking. In this paper we develop such a framework, combining local interactions with immigration from a regional species pool to derive community structure. This theoretical framework highlights the essential elements of these previous models.

One barrier to general theories of ecological communities is the 'curse of dimensionality': as the number of species  $\mathcal{N}$  goes up, the number of parameters typically goes up as  $\mathcal{N}^2$ . For realistically sized communities, this becomes unmanageable: there are more parameters than empiricists can measure and too many degrees of freedom for theoreticians to constrain their models. One theoretical solution is to choose parameters randomly (e.g., Barbier et al., 2018; May, 1972; Wilson & Lundberg, 2004), but this allows prediction only in an ensemble of replicate communities and is disconnected from the biology of how species interact with each other and their environment.

An alternative solution is to take a *trait-based* approach, where species are defined by the functional traits that determine their ecological performance (Litchman & Klausmeier, 2008; McGill et al., 2006). The closely related theoretical frameworks of evolutionary game theory (Brown & Vincent, 1987; McGill & Brown, 2007) and adaptive dynamics (Geritz et al., 1998) provide elegant tools for formulating and analysing trait-based models (reviewed in Klausmeier et al., 2020), but assume closed systems. While these trait-based approaches consider the interaction of a continuum of strategies and therefore have the potential to model diverse communities, the resultant evolutionarily stable communities (ESCs) are often species-poor unless extreme trade-offs are assumed (Edwards et al., 2018). Therefore, we apply the results of our general dispersal-selection theory to trait-based models in a metacommunity setting, where local dynamics are coupled to a regional pool of species through dispersal. This trait-based approach generates a broad range of testable predictions beyond the shape of the SAD—the traits of common versus rare species and how SADS vary along environmental gradients—which will enhance its falsifiability (McGill et al., 2007).

## GENERAL FRAMEWORK

Consider the general class of models of  $\mathcal{N}$  species, whose dynamics in a local community are given by

$$\frac{dN_i}{dt} = g_i(\vec{N})N_i + m_i \cdot (N_{R,i} - N_i) \quad (1)$$

$$\left[ \begin{array}{c} \text{change in} \\ \text{species } i \end{array} \right] = \left[ \begin{array}{c} \text{local} \\ \text{processes} \end{array} \right] + [\text{dispersal}]$$

where  $N_i$  is the abundance of species  $i$  (notation is summarised in Table G1). The first term describes local processes, where per capita growth rate  $g_i$  depends on the vector of all species,  $\vec{N} = (N_1, N_2, \dots, N_{\mathcal{N}})$ . The second term models dispersal at rate  $m_i$  between the local community and the broader region, where the species has fixed abundance  $N_{R,i}$ .

Setting Equation (1) equal to zero, we see that the equilibrium abundance of species  $i$  is determined by the balance of immigration versus emigration-plus-exclusion

$$\hat{N}_i = \frac{m_i N_{R,i}}{m_i + e_i} = \frac{[\text{immigration}]}{[\text{emigration}] + [\text{exclusion}]} \quad (2a)$$

with exclusion rate  $e_i \equiv -g_i(\vec{N})$ . Because the exclusion rate depends on the abundance of all species, a closed-form expression is typically impossible, so Equation (2a) typically must be studied numerically. However, we can derive analytical results in the limits of large and small dispersal to guide our understanding. When dispersal is large ( $m_i \rightarrow \infty$ ), it swamps local processes, so that each species simply matches its regional abundance:  $\hat{N}_i = N_{R,i}$ .

For simplicity, we assume that in the absence of dispersal ( $m_i = 0$ ) the community goes to equilibrium, where each species either persists ( $\hat{N}_{0,i} > 0$  and  $g_i = 0$ ) or goes extinct ( $\hat{N}_{0,i} = 0$  and  $g_i < 0$ ). We call species that persist in the absence of dispersal (*true*) *core species*. With even small dispersal, non-core species achieve positive abundance through mass effects. When they remain locally rare, we call them *satellite species* following Hanski (1982) (although we do not assume they are also regionally rare).

In the limit of small dispersal ( $m_i \approx 0$ ), the core species are unaffected by dispersal, while the abundance of satellite species can be approximated by

$$\hat{N}_i = \frac{m_i N_{R,i}}{e_{0,i}} \quad (2b)$$

where  $e_{0,i} = -g_i(\vec{N}_0)$  is the exclusion rate of species  $i$  in the closed system. Equivalently,

$$\log \hat{N}_i = \log m_i + \log N_{R,i} - \log e_{0,i} \quad (2c)$$

which suggests population sizes that vary over orders of magnitude, as in empirical SADs.

The universal observation that SADs consist of few common species and many rare species leads us to hypothesise that, using the appropriate currency for abundance (Morlon et al., 2009), common species represent core species while rare species represent satellite species dependent on continued dispersal from elsewhere to persist. Given this hypothesis, the bulk of SADs consists

of satellite species, whose abundances are determined by the balance of immigration and exclusion given by Equation (2), while the core species' abundances are determined mainly by local processes. Taking the dispersal rates  $m_i$  and the regional abundances  $N_{R,i}$  as given model parameters, the final ingredient that determines the SAD is the distribution of exclusion rates,  $e_i$ . Therefore, we must specify how species interact, which is encoded in the growth functions  $g_i(\vec{N})$  in Equation (1).

If we had detailed information on the interactions within a community such that we could parameterise the growth functions  $g_i(\vec{N})$ , we could predict how its SAD depends on dispersal with the regional metacommunity. However, these predictions would be specific to that particular system with defined interactions, limiting generality. Furthermore, such knowledge is typically lacking, particularly for species-rich communities. Therefore, to make general predictions about SADs, we need a reasonable way to parameterise models of diverse communities. Due to its solid basis in functional ecology (Litchman & Klausmeier, 2008; McGill et al., 2006; Violle et al., 2007), we use *trait-based* ecological theory (Klausmeier et al., 2020) to reduce the dimensionality of parameter-space in the rest of this paper.

## TRAIT-BASED MODELS

The fundamental assumption of trait-based models is that a species' demographic rates in a given abiotic/biotic environment depend only on its traits,  $\vec{x}_i$ . In this case, our general model (Equation 1) becomes

$$\frac{dN_i}{dt} = g(\vec{x}_i; \vec{N}, \vec{x}) N_i + m(\vec{x}_i) \cdot (N_{R,i} - N_i) \quad (3)$$

Note that the *growth function*  $g$  in Equation (3) is not species-specific, but shared by all species in a guild (Brown & Vincent, 1987). Therefore, species with identical traits have the same per capita growth rate, rendering them ecologically neutral at the local scale. The growth function  $g$  encodes density-dependence and interspecific interactions, possibly frequency-dependent, and depends on both the traits of the focal species,  $\vec{x}_i$ , and the abundances and traits of the entire community,  $\vec{N}$  and  $\vec{x}$ . The trait-based framework of Equation (3) is quite general. In the absence of dispersal, it has been used to model many ecological scenarios (reviewed in Klausmeier et al., 2020). Thus, diverse ecology can be encoded in the deceptively simple-looking  $g$ . The dispersal rate  $m$  can also depend on species traits or be assumed constant. The model is completed by describing the regional species pool through their traits  $\vec{x} = (\vec{x}_1, \vec{x}_2, \dots, \vec{x}_{\mathcal{N}})$  and abundances  $\vec{N}_R = (N_{R,1}, N_{R,2}, \dots, N_{R,\mathcal{N}})$ . For greater analytical tractability, instead of considering a large set of discrete species, we take a continuum limit, where

individuals are indexed by their trait values. Analogous to Equation (3), the general form of such a continuum model is

$$\frac{\partial n(\vec{x})}{\partial t} = g(\vec{x}, n(\cdot))n(\vec{x}) + m(\vec{x}) \cdot (n_R(\vec{x}) - n(\vec{x})) \quad (4)$$

for the dynamics of the local population-density  $n(\vec{x})$  of individuals with trait values  $\vec{x}$ , where  $n(\cdot)$  denotes the *local trait-abundance distribution* (TAD). Note that  $n(\vec{x})$  is the population density per unit trait, which differs from the  $N$  of particular species in Equation (3). E.g. with a single trait  $x$ , the integral  $\int_{x_1}^{x_2} n(x)dx$  gives the abundance of individuals with trait in the range  $x_1 \leq x \leq x_2$ . The regional species pool is described by the *regional TAD*  $n_R(\vec{x})$  and the *species-density function*  $\rho(\vec{x})$ , which describes how the species are distributed in trait-space (see Figure 1c). The species-density function is essential for converting from this continuum approach back to discrete species that constitute SADs (described in Box 1). Finally,  $m(\vec{x})$  is the potentially trait-dependent dispersal rate.

In the absence of dispersal ( $m(x) = 0$ ), methods from evolutionary game theory (Vincent & Brown 1987, Geritz et al., 1998) can be used to find the evolutionarily stable community (ESC; Edwards et al., 2018) representing the core species. Setting Equation (4) equal to zero, the equilibrium TAD with dispersal is formally given by

$$\hat{n}(\vec{x}) = \frac{m(\vec{x})n_R(\vec{x})}{m(\vec{x}) + e(\vec{x})} \quad (5)$$

where  $e(\vec{x}) \equiv -g(\vec{x})$  is the exclusion rate. Note that Equation (5) is not a closed-form solution to Equation (4), because the exclusion rate depends implicitly on the full TAD,  $\hat{n}(\cdot)$ .

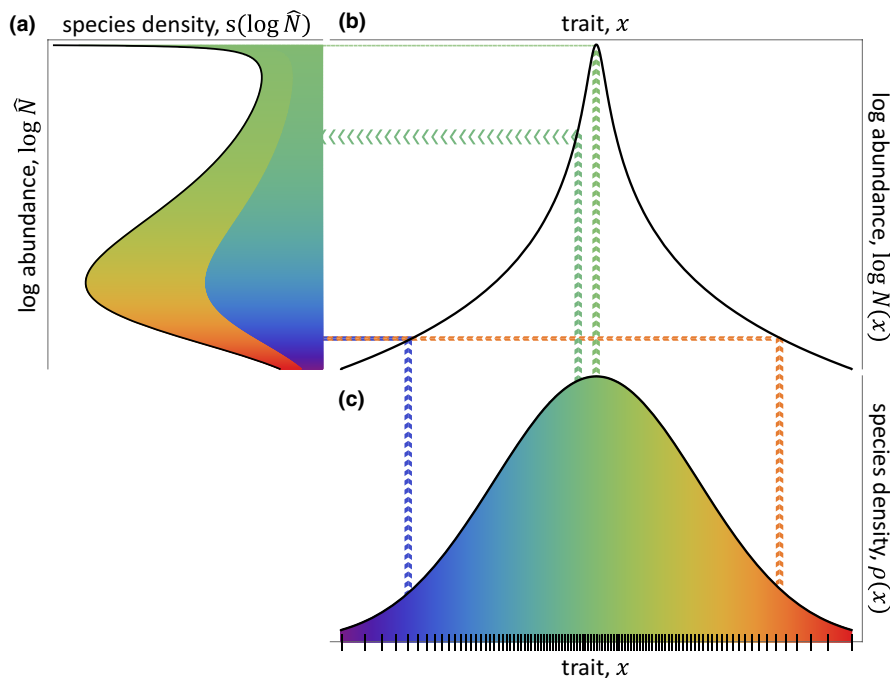
## Stabilising selection

To proceed further, we need to specify the functions  $g(x, n(\cdot))$ ,  $n_R(x)$ ,  $\rho(x)$  and  $m(x)$  (our examples are summarised in Table G2). For the growth function  $g$ , we will begin with one of the simplest ecological interactions: competition in a single niche, with a quadratic intrinsic growth function of a scalar trait,  $r(x)$ . This is an archetype of stabilising selection (Lande & Arnold, 1983) that is not only analytically tractable, but also useful as an approximation to more general situations. Defining  $N_{\text{tot}} = \int n(x)dx$  as the total abundance, this results in

$$g(x, n(\cdot)) = r(x) - aN_{\text{tot}} \quad (6a)$$

$$r(x) = r^* - \gamma(x - x^*)^2 \quad (6b)$$

where  $a$  is the competition coefficient that scales population sizes,  $r^*$  is the maximal growth rate at the optimal trait value  $x^*$  and  $\gamma$  quantifies the strength of stabilising selection. In the absence of dispersal (indicated by zero subscripts), there is a single-species ESC



**FIGURE 1** How the (a) Preston-plot SAD results from the transformation by (b) the TAD of (c) the regional species-density function (tick marks indicate discrete species). Flat parts of the TAD concentrate species density in the SAD, whereas sloped parts diffuse it (indicated by the width of the beams reflected off the TAD)



### BOX 1 Converting TADs to SADs

Converting the TAD  $n(x)$  to an SAD requires two steps, both of which require the species-density function,  $\rho(x)$ , describing the density of species along the trait axis. First, we must bin individuals from the continuous distribution  $n(x)$  into species abundances  $N(x)$ . Except where  $n(x)$  is sharply peaked relative to the spacing between species,  $\delta x(x) \equiv 1/\rho(x)$ ,  $N(x)$  can be well-approximated by  $N(x) = n(x)/\rho(x)$  (Appendix C).

Second, the log-transformed TAD,  $\log N(x)$ , can be used to translate the species-density function,  $\rho(x)$ , into a Preston plot SAD,  $s(\log N)$ . Mathematically, this is similar to transforming a random variable (Kobayashi et al., 2011). In general,

$$s(\log N) = \sum \frac{\rho(x(\log N))}{\left| \frac{d \log N}{dx} \right|} \quad (8)$$

where the sum is over all branches of the inverse function  $x(\log N)$ , because the log-TAD is typically non-invertible (see Appendix E for the case of multiple traits). Note that flatter parts of the log-TAD result in more species with that abundance and sloping parts result in fewer, due to the denominator (Figure 1).

In our example of a quadratic intrinsic fitness, one niche, trait-independent dispersal and uniform regional TAD and species density ( $\rho(x) = \rho$ ) (Figure 2), assuming  $N(x) = n(x)/\rho(x)$ , we find the SAD

$$s(\log N) = \rho w \frac{e^{\log N(x^*) - \log N}}{\sqrt{e^{\log N(x^*) - \log N} - 1}}$$

where  $N(x^*) = \hat{N}_{\text{tot}}/(\rho w \pi)$  is the height of the Lorentzian TAD at its peak.

Note that the SAD  $s(\log N)$  is a continuous distribution, which must be integrated to determine the number of species within a particular abundance range (McGill et al., 2007; Preston, 1948). In particular, the vertical asymptote(s) on the right side of our SADs represent core species when integrated.

(equivalently, a set of neutral species) with the optimal trait value  $x = x^*$  and total abundance  $\hat{N}_{\text{tot},0} = r^*/a$ , leading to a TAD consisting of a Dirac delta function,  $\hat{n}_0(x) = \hat{N}_{\text{tot},0} \delta(x - x^*)$ .

Further assuming trait-independent dispersal  $m(x) = m$  and a uniform regional TAD  $n_R(x) = n_R$ , we find that the equilibrium TAD is

$$\hat{n}(x) = \hat{N}_{\text{tot}} \frac{w/\pi}{w^2 + (x - x^*)^2} \quad (7a)$$

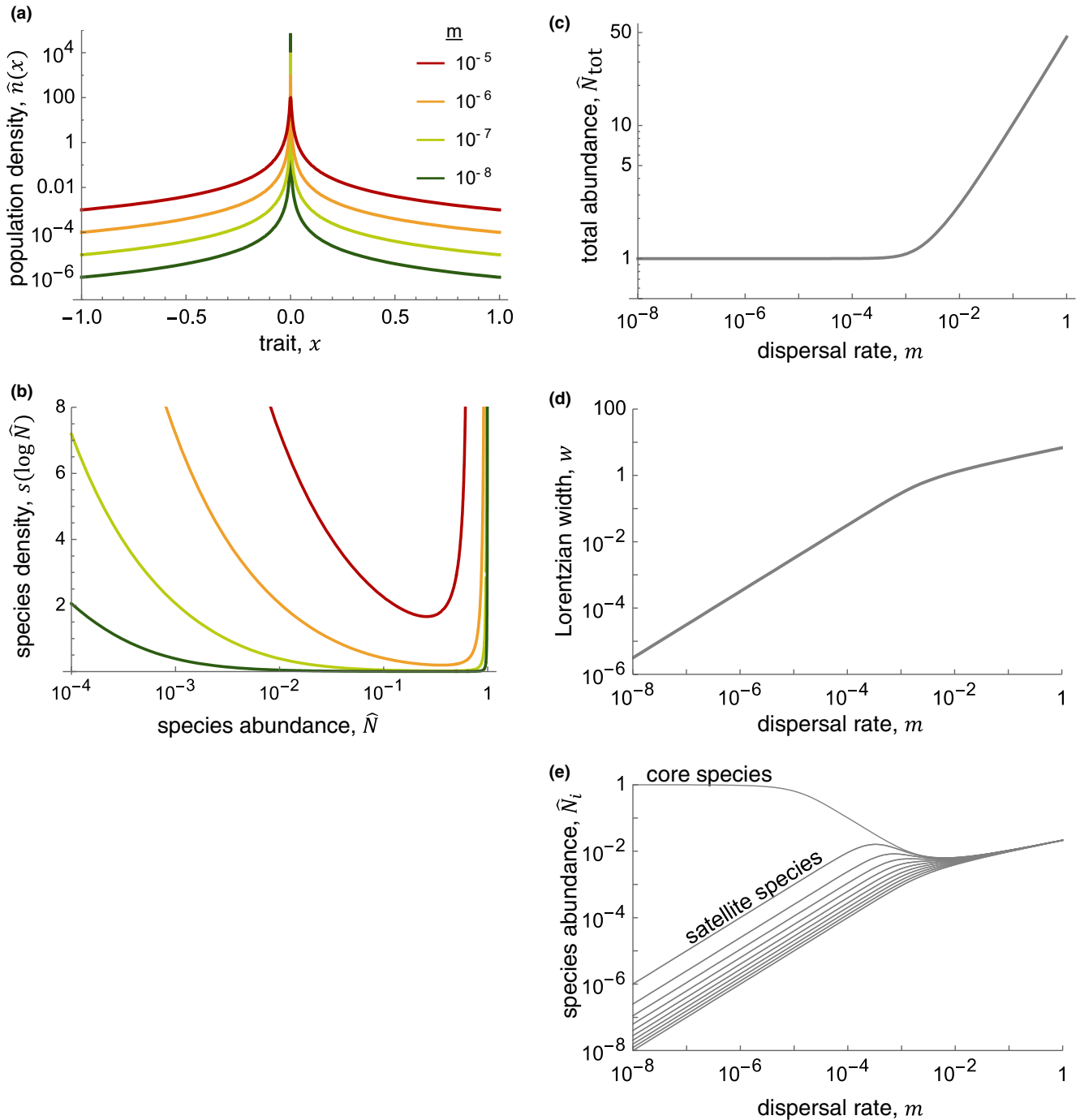
$$w = \frac{\pi m n_R}{\gamma \hat{N}_{\text{tot}}} \quad (7b)$$

This is still not a closed-form solution, because the total abundance  $\hat{N}_{\text{tot}}$  is not explicitly defined, but it shows that the TAD takes the form of a Lorentzian function, with characteristic width  $w$ . Lorentzians are bell-shaped curves superficially similar to Gaussians, but are heavy-tailed with a power-law exponent of  $-2$  (Figure 2a). Bürger (2000) found a Cauchy distribution in a mutation-selection balance model analogous to this situation.

In Appendix A we show that the total abundance  $\hat{N}_{\text{tot}}$  is the solution of a cubic equation, whose explicit form is non-insightful but is used for plotting results below. In

the limit of low dispersal, it can be well-approximated as  $\hat{N}_{\text{tot}} \approx \hat{N}_{\text{tot},0}$ , and in the limit of high dispersal as  $\hat{N}_{\text{tot}} \approx \pi \sqrt{\frac{m}{\gamma}} n_R$ , with a cross-over between these regimes around  $m_c \approx \frac{\sqrt{r^* \gamma} \hat{N}_{\text{tot},0}}{\pi n_R}$  (Figure 2c). Note that total abundance diverges in the high dispersal limit ( $\hat{N}_{\text{tot}} \rightarrow \infty$  as  $m \rightarrow \infty$ ) in this simple example due to our assumption of uniform regional abundance, since  $\hat{N}_{R,\text{tot}} = \int_{-\infty}^{\infty} n_R(x) dx = \infty$ . Therefore, the low dispersal limit ( $m < m_c$ ) is more relevant here; other examples with finite regional abundance are well-behaved in both limits.

Figure 2 shows the effect of dispersal rate  $m$  on the equilibrium TAD  $\hat{n}(x)$  and SAD  $s(\log \hat{N})$ , derived from the TAD following Box 1. The SAD has an increasing left-tail and a thin asymptote on the right, which represents the single core-species (Figure 2b). As in the discrete-species case (Equation 2a), the abundance of satellite species is proportional to dispersal rate (Figure 2a,e). The width of the Lorentzian  $w$  increases with dispersal, as seen in Equation (7b) (Figure 2d). Total abundance  $\hat{N}_{\text{tot}}$  is approximately constant in the low dispersal regime (Figure 2c), which implies that the density within the expanding core must decrease with dispersal (Figure 2a). Therefore, for species with a trait value close to the true core species, density first increases linearly, then decreases as it enters



**FIGURE 2** Our first example (one niche, quadratic fitness function, uniform regional TAD). Equilibrium (a) TADs and (b) SADs for four dispersal rates  $m$ . (c–e) the effect of dispersal on (c) total abundance  $\hat{N}_{\text{tot}}$ , (d) width of the Lorentzian TAD  $w$  and (e) abundance of 21 evenly spaced species between  $x = -1$  and  $x = 1$ . Parameters:  $a = 1$ ,  $r^* = 1$ ,  $x^* = 0$ ,  $\gamma = 1$ ,  $n_R(x) = 100$ ,  $\rho(x) = 100$  so that  $N_R(x) = 1$ .

the core community (Figure 2e). In Appendix A we show that the core community with dispersal can be defined as species within the characteristic width of the Lorentzian  $w$  of the true core species (equation [A16]).

### Effect of regional species pool

The assumptions of uniform regional TAD  $n_R(x)$  and species-density distribution  $\rho(x)$  made above facilitate

analytical calculations, but are unrealistic, so that strictly Lorentzian TADs represent a special case. First, consider a non-uniform regional TAD. In this case, the regional TAD  $n_R(x)$  undergoes a Lorentzian-like transformation by the exclusion rate  $e(x)$  (Equation 5). Under the assumptions of stabilising selection (Equation 6) and trait-independent dispersal, this results in the equilibrium TAD

$$\hat{n}_i(x) = \frac{mm_R(x)}{m + a\hat{N}_{\text{tot}} - r^* + \gamma(x - x^*)^2} \quad (9)$$

As before, this is not a closed-form solution due to the presence of the total abundance  $\hat{N}_{\text{tot}}$ . Although  $\hat{N}_{\text{tot},0}$  remains a good approximation at low dispersal rates, unfortunately, in general  $\hat{N}_{\text{tot}}$  must be determined numerically. Note that in the absence of selection (neutrality,  $\gamma = 0$ ), the local TAD is proportional to the regional TAD if dispersal is the same for all species.

Second, the technique given in **Box 1** can be used to derive SADs from TADs in the case of non-uniform species density. As an example, consider a Gaussian species-density distribution,  $\rho(x) = \rho^* / (\sigma_\rho \sqrt{2\pi}) \exp(-x^2 / (2\sigma_\rho^2))$ , where the density of species decreases away from the origin (**Figure 3a**). Assuming uniform regional species abundances  $N_R(x) = N_R$ , the regional TAD is proportional to  $\rho(x)$ :  $n_R(x) = N_R \rho(x)$ . In this case, the TAD has a narrow spike at the optimal trait value (**Figure 3b**); it superficially resembles that of our previous example (**Figure 2a**), but decreases more sharply due to the lower regional abundance away from  $x = 0$ . However, in contrast to the case of uniform regional TAD, the resulting SAD is now unimodal (**Figure 3c**), due to the low density of species in the tails of the species-density distribution  $\rho(x)$ .

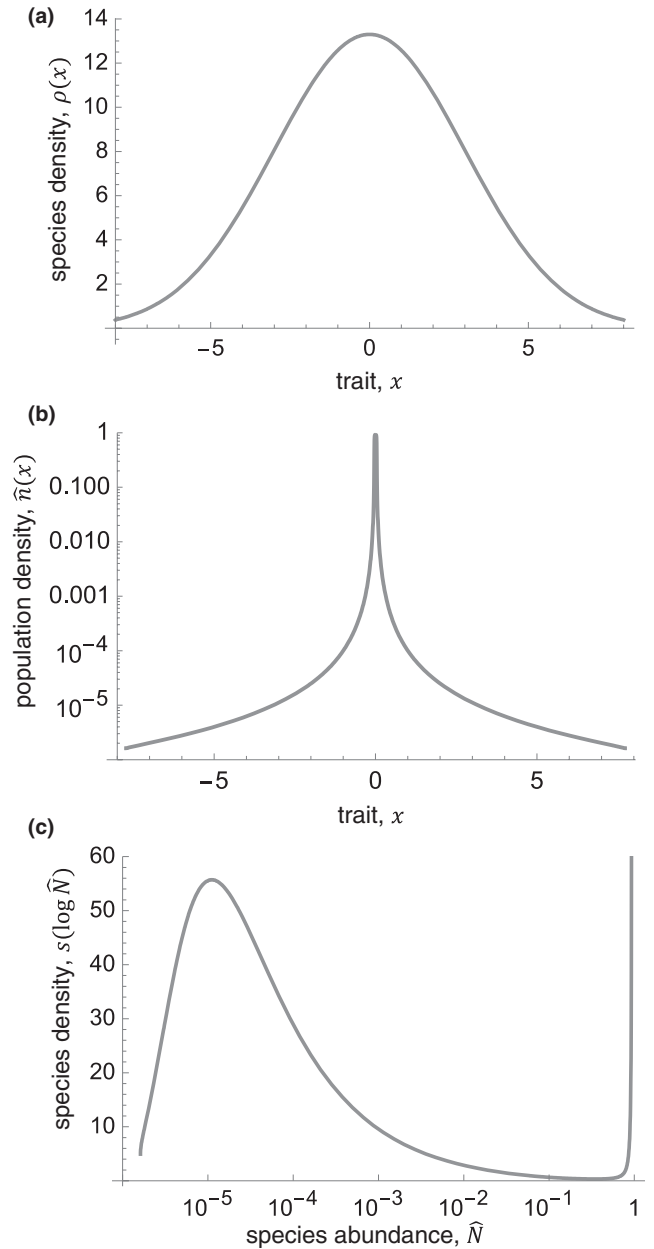
### Other interaction models (non-quadratic $r$ , multiple niches)

The previous examples all assume one niche and a quadratic intrinsic fitness function (Table G2), representing an analytically tractable model of stabilising selection. However, our general trait-based framework of **Equation (4)** is applicable to a much wider range of ecological scenarios, including frequency-dependent interactions. Here, we give two more examples to show how the details of local interactions affect TADs and SADs. Although no analytical results are available in general, these TADs can be approximated as Lorentzians near a peak (**Appendix B**).

First, consider one niche but a Gaussian intrinsic fitness function,  $r(x) = r^* \exp(-x^2 / (2\sigma_r^2))$ . This can be applicable if the trait affects fitness only through the birth rate, which must be non-negative, making the fitness function bounded from below. **Figure 4a** shows that the equilibrium TAD is peaked around the optimum  $x = 0$  but is also bounded from below. This can be understood from the exclusion rate at equilibrium (**Figure 4b**), which approaches a constant maximum value, no matter how maladapted a species is. This flat range of the TAD translates into the vertical asymptote at  $\hat{N} = 10^{-5}$  on the left side of the SAD (**Figure 4c**).

Finally, we relax the assumption of frequency independence by letting the strength of competition  $a$  decline with the difference in traits between interacting species. That is,

$$g(x, n(\cdot)) = r(x) - \int a(x, x') n(x') dx' \quad (10a)$$

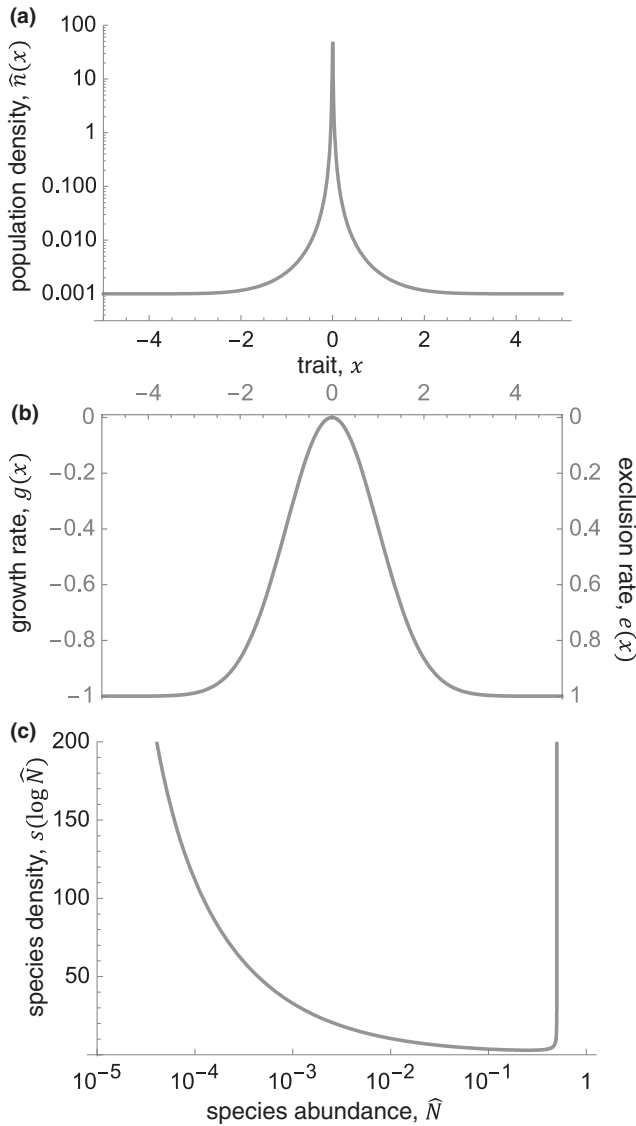


**FIGURE 3** Our second example (one niche, quadratic fitness function, Gaussian species-density function and therefore Gaussian regional TAD). (a) Species-density function, (b) local TAD and (c) unimodal SAD. Parameters as in **Figure 2** except  $\sigma_\rho = 3$ ,  $\rho^* = 100$ ,  $N_R = 1$ ,  $m = 10^{-4}$ .

$$a(x, x') = a_0 \exp\left(-\frac{(x-x')^2}{2\sigma_a^2}\right) \quad (10b)$$

This trait-based Lotka–Volterra competition model is a classic model for niche differentiation (e.g. Ranjan & Klausmeier, 2022; Scheffer & van Nes, 2006). In the absence of dispersal, when  $\sigma_a < \sqrt{r^* / (2\gamma)}$  there is an evolutionarily stable community (ESC) consisting of more than one species (Ranjan & Klausmeier, 2022). In our example, the ESC consists of three evenly spaced





**FIGURE 4** Our third example (one niche, gaussian fitness function, uniform regional TAD). (a) TAD, (b) growth/exclusion rate, (c) SAD. Parameters as in Figure 2 except  $\sigma_r = 1, m = 10^{-5}$ .

core species that sit at local invasion fitness maxima (Figure 5a).

Because the continuum model Equation (4) would need to be discretised before solving numerically, we directly simulate Equation (3) with a discrete set of species. With small dispersal, the TAD has three locally Lorentzian peaks (Figure 5b), whose heights and widths are largely determined by the non-dispersal abundance and curvature of the fitness function (Appendix B). Overall, the TAD is determined by equation (5), with the exclusion rate playing the central role given our assumption of uniform regional TAD and species density (Figure 5c). Because the exclusion rate for species between the three core species is very small (on the order of  $10^{-3}$ ), it takes only a small immigration rate to boost these nearly neutral species to appreciable densities (Figure 5b).

Like the TAD, the SAD is multimodal (Figure 5d): the two rightmost peaks in the SAD correspond to the peaks in the TAD (two of which have the same height), whereas the third peak from the right in the SAD corresponds to the local minima of the TAD. However, this fine detail may be difficult to detect in empirical SADs. Figure 5e shows a SAD fitted using kernel density estimation on a discrete set of  $\mathcal{N} = 401$  species, indicated by ticks on the  $x$ -axis. The narrow peaks of the theoretical SAD (Figure 5d) cannot be distinguished, merging into one wide peak.

### Controls on the distribution of satellite species

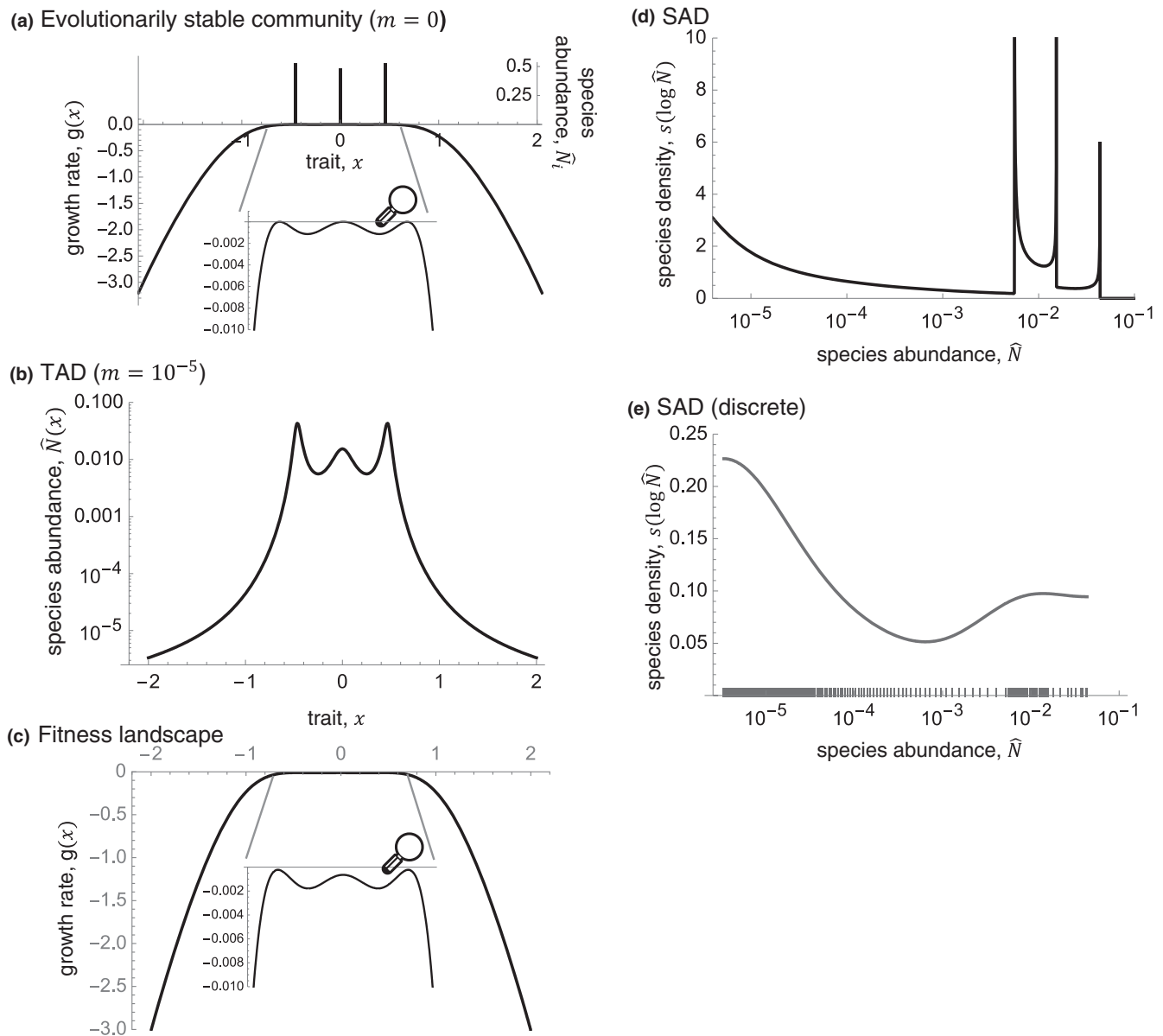
Because most species in local communities are rare, we can understand the bulk of TADs and SADs by focusing on the satellite species, greatly simplifying the analysis (Appendix D). Of particular historical interest is the behaviour of the SAD's left tail, which describes the relative abundance of rare species (McGill et al., 2007 pp. 1004–5). Assuming  $N(x) \rightarrow 0$  as  $x \rightarrow \pm \infty$ , we find that if the species-density function  $\rho(x)$  decays faster than a power law, then  $s(\log N) \rightarrow 0$  as  $N \rightarrow 0$ , as the Gaussian  $\rho(x)$  does in Figure 3c. If it decays more slowly, as a power law, then the SAD's left tail depends on exponent of the regional population-density function and the exclusion function:

$$\lim_{N \rightarrow 0} s(\log N) = \begin{cases} 0 & \alpha_\rho + \max[\beta_e, \beta_{N_R}] > 1 \\ \infty & \alpha_\rho + \max[\beta_e, \beta_{N_R}] < 1 \\ \text{const.} & \alpha_\rho + \max[\beta_e, \beta_{N_R}] = 1 \end{cases} \quad (11)$$

A special case: if  $\rho(x)$  and  $N_R(x)$  are constant, then  $s(\log N) \rightarrow 0$  if the exclusion function  $e_0(x)$  increases faster than exponentially and  $s(\log N) \rightarrow \infty$  if it declines slower than exponentially (as in Figure 2b).

## DISCUSSION

What determines the shape of SADs? Our analysis suggests that the simple answer is ‘there is no simple answer’. Both local processes (environmental filtering and species interactions) and the properties of the regional species pool (species abundances and traits) jointly determine the distribution of commonness and rarity in a community. These factors span from local to landscape and biogeographic scales, each subject to tremendous variation and historical idiosyncrasy. Therefore, it seems highly unlikely that there is a universal, parameter-sparse SAD applicable across all communities. Despite the manifold variety of possible SADs it can produce, our framework identifies key factors that shape them—rates of exclusion and dispersal,



**FIGURE 5** Our fourth example (localised competition, quadratic fitness function, uniform regional TAD). (a) the evolutionarily stable community reached in the absence of dispersal and the corresponding invasion-fitness landscape. (b) TAD with dispersal and (c) the corresponding fitness landscape. (d) Continuum-based SAD. (e) Discrete-species-based SAD. Parameters as in Figure 2 except:  $a_0 = 1$ ,  $\sigma_a = 0.4$ .

regional population abundance and the species-density distribution.

## Empirical predictions

Our framework makes a number of empirically testable predictions, outlined below in order of increasing specificity and data requirements. The first three predictions follow from the solution to the general model (Equation 2) and require only SADs (prediction 1) and measurements of dispersal (prediction 2) or exclusion rates (prediction 3). Predictions from the trait-based framework (Equation 3) require data on species traits as well as SADs (both local and regional). Finally, predictions from system-specific

models require detailed understanding of how species interact to parameterise a particular growth function  $g$ . Thus, our framework can be tested at multiple levels of generality, using observational data as well as experiments.

First, although our framework can produce a multitude of SAD shapes, some general predictions exist. It predicts that at low dispersal rates, the SAD will have a gap between the most-abundant core species and the rare species that make up the bulk of the community. It also can explain multimodal SADs (Antão et al., 2017; Dornelas & Connolly, 2008), generalising the findings of Vergnon et al. (2012) and Rael et al. (2018). If the scaling exponents of the exclusion function and the regional species pool are known, it predicts the behaviour of the left-hand tail of the SAD (rare species) (Equation 11).

Second, it predicts that at low immigration rates, the abundance of rare satellite species will vary linearly with the immigration rate (Equation 2b), while the abundance of common core species will be largely unaffected (Figure 2e). The increase of rare species in a meta-analysis of SADS is consistent with this prediction (Jones et al., 2020). An important corollary is that satellite species cannot persist in the absence of immigration. The immigration rate is the product of the dispersal rate  $m_i$  and the regional abundance  $N_{R,i}$ . High dispersal leads the local community to converge with the regional metacommunity (Equation 2a). These predictions could be tested by manipulating the immigration rate experimentally. Patrick (1967) showed that increased immigration led to SADS with more rare species of stream diatoms. Further experimental tests in different systems are needed.

Third, it predicts that the exclusion rate (negative invasion/growth rate) strongly affects species abundances. Invasion rate is a central concept in ecological theory and can be experimentally measured in a number of ways (Grainger et al., 2019), providing another way to test the general framework.

Fourth, our trait-based framework predicts that the identity and abundance of dominant core species will be determined by their traits and environmental conditions. Empirical support for this prediction comes from tropical forests (Umaña et al., 2015) and prairies (Harpole & Tilman, 2006). In contrast to neutral theory, replicate local communities with similar environmental conditions should have the same dominant species. The most informative observational evidence would come from cases where the local communities deviate strongly from the regional metacommunity, since neutral theory predicts that regionally abundant species will also tend to be locally abundant. Experimental manipulation of environmental conditions or starting new communities would provide an even more powerful test of this prediction.

More-specific models can generate more-specific hypotheses. Our general framework can accommodate a wide variety of particular models through the growth function  $g$ , leveraging the broad knowledge-base of trait-based ecological theory (Klausmeier et al., 2020). Predictions of how TADs and SADS change along environmental gradients, such as nutrient and stress gradients, can be made by varying environmental parameters. Verbal hypotheses for how SADS should vary with pollution (Gray, 1979) could be made more precise, and predictions for how community-weighted trait moments vary along environmental gradients could be made.

## Population-dynamic SAD theories

Population-dynamic theoretical explanations of SADS invoke one (or both) of two alternative sources of variation in species abundance: *chance* and *fate*. In chance-based explanations, species have identical parameters (symmetric

models, which include non-interacting species and neutral models as special cases) but include either environmental (Engen & Lande, 1996a, 1996b) or demographic stochasticity (Hubbell, 2001; Kendall, 1948). In fate-based explanations, dynamics are deterministic, but species have different parameters, either randomly assigned (Wilson et al., 2003; Wilson & Lundberg, 2004; Zhou & Zhang, 2008) or determined by traits (Vergnon et al., 2012, our approach). A few models combine both sources of variation (Haegeman & Loreau, 2011; Hughes, 1986; Rael et al., 2018). While both approaches can produce realistic SADS, an important distinction concerns the role of species identity. In chance-based explanations, all species will eventually experience the entire range of abundances in the SAD, whereas in fate-based explanations, species will be consistently common or rare in a particular environment. This could be tested with time series of SAD dynamics. Our population-dynamic approach complements McGill's (2011) top-down approach of treating local SADS as clumped random samples of a regional SAD, by providing an explicit mechanistic basis for clumping.

## Model assumptions

Of Vellend (2010) four fundamental processes that shape ecological communities, our approach is based on selection and dispersal. Because we focus on local community dynamics on ecological timescales, we do not explicitly model speciation, but it can be considered implicitly as a determinant of the regional species pool.

Selection embodies diverse interspecific interactions with a seemingly endless number of variations, from abstract, general models like Lotka–Volterra, to those tailored to particular ecosystems. Indeed, the majority of ecological theory includes only selection, due to its inherent richness. Although our examples are based on Lotka–Volterra competition, our analytical framework (general, Equation 1; assuming trait-based interactions, Equation 3) can be applied to a much wider range of ecological scenarios through the growth function  $g$  (see Appendix F for an example with specialised natural enemies).

Dispersal, in particular immigration from the regional metacommunity, plays a central role in shaping local community structure through mass effects (Shmida & Wilson, 1985). Consistent with our theory, Murray et al. (1999) found that 91–95% of locally rare plant species were abundant at another site within their range. While some studies invoke immigration to explain rare transient species in the left-hand tail of SADS (Magurran & Henderson, 2003), previous theory has shown that even a small amount of immigration can translate into large populations of weakly excluded species (Pulliam, 1988; Gonzalez & Holt, 2002). This inflationary effect can be seen in previous models of SADS (Gravel et al., 2006; Hughes, 1986; Kendall, 1948; Loreau & Mouquet, 1999; Scheffer & van Nes, 2006) and forms the basis of our analytical theory (Equation 2).

We model dispersal as the exchange of individuals between a local community and the regional metacommunity (Hubbell, 2001; McGill, 2011). Species interact on the local scale, whereas the regional scale covers the range of dispersing individuals. As common in community ecology, these discrete scales are not precisely defined, but depend on the natural history of the organisms and the interests of the investigator. By treating the regional metacommunity as exogenous, we can gain general insights into the role of immigration applicable across a range of spatial settings (island-mainland, true metacommunity, continuous landscape). Coupling multiple local communities so that the regional metacommunity emerges from internal system dynamics (Mouquet & Loreau, 2003) is an important next step.

Unlike neutral theory (Hubbell, 2001), we neglect ecological drift (demographic stochasticity). The primary reason is to contrast fate-based explanations of SADs with chance-based explanations. Demographic stochasticity is most important in small populations, so our approach is most suitable for communities with high total abundance, but may need to consider drift of the rarest species. Future research that integrates all three fundamental ecological processes (selection, dispersal and ecological drift) can build off the analytical foundations of our current framework. In particular, rare satellite species that do not affect others can be modelled as independent birth-death-immigration processes, leading to negative-binomially distributed abundances (Kendall, 1948), which might explain the relative variability of rare species (Henderson & Magurran, 2014).

Because we focus on the theoretical processes underlying SADs, we also neglect random variation in empirical SADs due to the sampling process, which will be required for rigorous comparison with empirical data (Bulmer, 1974). We anticipate the effect of limited sampling will be qualitatively similar to the unveiling of the log-normal distribution noted by Preston (1948).

## Implications

The fitness (growth) function is a central concept in eco-evolutionary frameworks such as adaptive dynamics (Geritz et al., 1998). However, the fitness function is often used only as a means towards the end of determining the evolutionarily stable community (ESC) (Brown & Vincent, 1987; Klausmeier et al., 2020). With immigration from the regional metacommunity, the ESC represents the bones of the community (core species), while the fitness function helps shape the flesh (satellite species). Rather than being ultimately discarded as in adaptive dynamics, the fitness function itself is a key result providing valuable information on the distribution of satellite species in the presence of immigration.

Our framework connects SADs with species- and trait-based community models, setting the stage for future theoretical extensions, including incorporating

non-equilibrium dynamics (random: Chesson, 2000, seasonal: Kremer & Klausmeier, 2017) and structured populations (discrete: Caswell, 2001, continuous: De Roos & Persson, 2001) into SAD theory. Appendix F adds top-down control by specialised natural enemies to our first example. While we have focused on long-term equilibrium behaviour, models such as Equations 1 and 3 can also be used to study transient dynamics (DeAngelis & Waterhouse, 1987; Hastings, 2004). Thus, our framework lays a general theoretical foundation for the study of SADs, allowing them to become fully integrated into the mainstream of theoretical ecology.

## AUTHORSHIP

TK, KU and CAK developed theory. TK wrote the first draft of the manuscript, CAK revised it, all authors contributed substantially to further revisions. CAK & EL obtained funding.

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## PEER REVIEW

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## DATA AVAILABILITY STATEMENT

No data were used in this study. The Mathematica code supporting our analysis and used to generate the figures is archived at <https://doi.org/10.5281/zenodo.6954673>

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## SUPPORTING INFORMATION

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