



Emergent niche structuring leads to increased differences from neutrality in species abundance distributions

ROSALYN C. RAEL,^{1,2,5} RAFAEL D'ANDREA,^{1,3} GYÖRGY BARABÁS,^{1,4} AND ANNETTE OSTLING¹

¹*Ecology and Evolutionary Biology, University of Michigan, 830 North University, Ann Arbor, Michigan 48109-1048 USA*

Abstract. Species abundance distributions must reflect the dynamic processes involved in community assembly, but whether and when specific processes lead to distinguishable signals is not well understood. Biodiversity and species abundances may be shaped by a variety of influences, but particular attention has been paid to competition, which can involve neutral dynamics, where competitor abundances are governed only by demographic stochasticity and immigration, and dynamics driven by trait differences that enable stable coexistence through the formation of niches. Key recent studies of the species abundance patterns of communities with niches employ simple models with pre-imposed niche structure. These studies suggest that species abundance distributions are insensitive to the relative contributions of niche and neutral processes, especially when diversity is much higher than the number of niches. Here we analyze results from a stochastic population model with competition driven by trait differences. With this model, niche structure emerges as clumps of species that persist along the trait axis, and leads to more substantial differences from neutral species abundance distributions than have been previously shown. We show that heterogeneity in “between-niche” interaction strength (i.e., in the strength of competition between species in different niches) plays the dominant role in shaping the species abundances along the trait axis, acting as a biotic filter favoring species at the centers of niches. Furthermore, we show that heterogeneity in “within-niche” interactions (i.e., in the competition between species in the same niche) counteracts the influence of heterogeneity in “between-niche” interactions on the SAD to some degree. Our results suggest that competitive interactions that produce niches can also influence the shapes of SADs.

Key words: *coexistence; community assembly; competition; Lotka-Volterra model; neutral theory; trait axis.*

INTRODUCTION

A question debated in community ecology is whether the pattern of species abundances in a given community reflects underlying mechanisms involved in assembling it or instead reflects only broad mechanisms common not only across communities, but to a variety of complex systems (Nekola and Brown 2007). Neutral theory (Bell 2000, Hubbell 2001) and niche differentiation (Chesson 1991, 2000, Leibold 1995, Chase and Leibold 2003, Meszéna et al. 2006) provide different hypotheses for mechanisms that drive the patterns of diversity and abundance we see in nature. The principle of competitive exclusion says that species must be sufficiently different from each other with regard to traits relevant to competition in order to coexist (Hardin 1960). Competitive exclusion can be exemplified by Lotka-Volterra competition models, which predict that species that are sufficiently different can coexist stably and can invade populations of other species from low abundance (MacArthur and Levins 1967, May 1973). On the other hand, neutral theory suggests that coexistence is more influenced by

species' similarity rather than their differences, with similarity allowing species to persist together for long periods of time (Chesson 2000, Hubbell 2001). Neutral theory then posits that in any given local community immigration maintains diversity by balancing extinction events that eventually occur due to stochasticity (Hubbell 2001, Volkov et al. 2005). Even though the nature of coexistence differs in communities with neutral versus niche dynamics, recent studies have suggested that the species abundance distributions (SADs) of these two types of communities are too similar to be used to infer the presence of niche structure (Chave et al. 2002, Mouquet and Loreau 2003, Purves et al. 2005, Chisholm and Pacala 2010, Haegeman and Loreau 2011, Pigolotti and Cencini 2013, Carroll and Nisbet 2015).

Many of the recent studies considering the differences between niche and neutral SADs have mainly considered whether niche and neutral community assembly modes produce SADs within the same range of forms as model parameters are varied (Chave et al. 2002, Mouquet and Loreau 2003, Pigolotti and Cencini 2013). Neutral models in ecology consist of immigration from a “metacommunity” source pool to a local community where the SAD is determined by the number of species and the rates of speciation and dispersal (Hubbell 2001). Speciation and dispersal rates in particular are difficult to measure and are therefore treated as free parameters of the neutral model, which is fit to observations. In this case, significant differences in the ranges of SADs that niche and neutral dynamics yield might suggest that empirical SADs can give insight into the underlying processes shaping the community. However, if speciation and dispersal rates could be estimated using data, then more

Manuscript received 22 November 2017; revised 27 February 2018; accepted 21 March 2018. Corresponding Editor: Tom E. X. Miller.

²Present address: ByWater Institute, Tulane University, 6823 St. Charles Avenue, New Orleans, Louisiana 70118 USA.

³Present address: Department of Plant Biology, University of Illinois at Urbana-Champaign, 505 South Goodwin Avenue, Urbana, Illinois 61801 USA.

⁴Present address: Division of Theoretical Biology, Department IFM, Linköping University, SE-58183 Linköping Sweden.

⁵E-mail: rosaly.n.rael@gmail.com

specific neutral SAD predictions could be made based on those parameter values and compared with data. The relevant theoretical question for whether observed SADs are useful for insight into underlying processes is then whether there are differences between the particular niche and neutral SADs produced with the same parameter values. In fact, information is becoming increasingly available on dispersal rates (Clark et al. 1999, Muller-Landau 2001), as is data that could be used to approximate the abundance distribution of the regional pool in a neutral model and estimate speciation rate. For example, data is becoming available on the abundances of tree species in a large region of the Panama basin surrounding Barro Colorado Island (Hubbell et al. 2005) that might serve this purpose. Furthermore, if SADs were known to be more revealing of underlying processes when parameters are measurable, this might motivate further collection of dispersal and regional abundance data. Hence a comparison is warranted between niche and neutral SADs with fixed dispersal and speciation parameters to see if SADs might reveal the presence of non-neutral processes when parameters are known.

Some recent studies have considered differences between niche and neutral SADs occurring for fixed speciation and immigration parameters. They conclude that a large amount of niche structuring is needed to create substantial differences between niche and neutral SADs. For example, Purves et al. (2005) and Chisholm and Pacala (2010) considered a simplified, extreme, niche structure in which species fall into discrete, non-interacting guilds within which they interact neutrally. Chisholm and Pacala (2010) showed that this type of stochastic niche model produces SADs that are virtually indistinguishable from the neutral SAD when species richness is much higher than the number of niches, and that it takes a large number of niches to obtain substantial differences between niche and neutral cases. Haegeman and Loreau (2011) and Pigolotti and Cencini (2013) came to the same conclusion when considering another type of simplified niche structure in which intraspecific and interspecific competition were each respectively determined by a single parameter. They found that SADs change little as a small amount of niche structure is enforced by strengthening intraspecific relative to interspecific competition.

However, it may be premature to draw conclusions about the community abundances typically expected in nature from these studies, as real interaction structures are expected to be more complex than the ones in the models described above. In particular, empirical evidence supports trait distance as a key determinant of the strength of competition (Johansson and Keddy 1991, Jiang et al. 2010, Burns and Strauss 2011). This is what one would expect if there is an array of resources or "limiting factors" (Levin 1970, Meszena et al. 2006) for competing species to partition based on continuous trait values. For example, water and nutrients available at different soil depths might be used differently across plant species that differ in their root depth (Silvertown 2004). Available patches of different ages since disturbance might be exploited differently across tree species that differ in their life history strategies (Kohyama 1993). In these examples, species with similar traits should compete more strongly because they will consume available resources or interact similarly with "limiting factors." Recent theoretical studies

show that competitive interactions driven by species' differences along a trait axis typically lead to niche structuring in the form of persistent clusters of similar species (Bonsall et al. 2004, Holt 2006, Scheffer and van Nes 2006, Pigolotti et al. 2007, Ernebjerg and Kishony 2011, Segura et al. 2011, Vergnon et al. 2012, D'Andrea and Ostling 2016). These clusters emerge from the dynamics themselves instead of being externally imposed. The niche dynamics studied by Purves et al. (2005) and Chisholm and Pacala (2010) could be viewed as a possible limiting case of this expected structure, with identical competitors (neutral dynamics) within clusters, but no interaction at all between clusters.

Here we consider SADs in a stochastic competition model in which structuring of species into niches emerges rather than being imposed. Specifically, we consider a stochastic version of the classic Lotka-Volterra competition model along a trait axis, where interaction strength declines with interspecific trait difference, a simple model that captures arguably the most salient feature of competition structuring many ecological communities. This model predicts system-specific limits to the similarity of coexisting species (MacArthur and Levins 1967, May 1973, Abrams 1983, Szabo and Meszena 2006, Barabas and Meszena 2009, Barabas et al. 2012, 2013a). Perhaps counterintuitively, the transient state of the Lotka-Volterra model involves emergent clustering of species on the trait axis (the species nearest to those that coexist at equilibrium take the longest to be excluded). The addition of intraspecific negative density dependence, environmental fluctuations, or mutation typically make clustering created by competitive interactions persistent. This "self-organized similarity" or "emergent neutrality" was highlighted in a variety of recent studies (Bonsall et al. 2004, Holt 2006, Scheffer and van Nes 2006, Vergnon et al. 2009, 2012, Ernebjerg and Kishony 2011, Segura et al. 2011), and reviewed in D'Andrea and Ostling (2016). Some recent studies have highlighted observed clumped patterns of species on trait axes in support of those consistent with an emergent niche perspective (Vergnon et al. 2009, Yan et al. 2012, Segura et al. 2013). We use a stochastic version of the Lotka-Volterra model with immigration that produces a persistent pattern of emergent clusters (Barabas et al. 2013b) through "mass effects" (Leibold et al. 2004), whereby immigration counteracts competitive exclusion and produces higher average abundances in species that would be excluded more slowly. These emergent clusters can be viewed as separate "niches" in the sense that species at the centers of these clusters would stably coexist with one another.

We use our model to consider the potential for niche dynamics to produce different SADs than the neutral case when speciation and dispersal parameters are fixed. We also compare differences from SADs produced by the extreme niche model of Chisholm and Pacala (2010), which we will refer to as the CP model throughout this paper. We also demonstrate that the heterogeneity in interaction strength deriving from the dependence of competition on trait differences in our model is shaping the SAD. We show that heterogeneity in interactions between species in separate niches is important in driving the observed species abundance patterns, even though between-niche interactions are weaker than within-niche interactions. This study lays the

groundwork for further investigations on the distinguishability of niche and neutral assembly modes using SADs and other community patterns when niches emerge rather than being imposed. Furthermore, it highlights the necessity of understanding the competitive interactions and emergent niche structures that occur in nature for continued development of a stochastic niche theory for SADs and other community properties.

MODEL AND SIMULATION METHODS

We use the spatial structure often used in neutral models in ecology consisting of a “metacommunity” pool of species that can immigrate into a smaller local community (Hubbell 2001). We focus on the influence of niche differentiation on SADs only in the local community. We do not incorporate niche differentiation into the source pool, or model its dynamics explicitly. Instead we assume the relative abundances of species in the source pool follow a Ewens sampling distribution, as would be expected for an infinite metacommunity governed by the standard neutral model involving point speciation (Etienne et al. 2007). We model immigration from this source pool as stochastic, and model the dynamics of the species in the local community as a stochastic implementation of the standard Lotka-Volterra competition differential equations, where the strength of competition is a function of the distance between competitors’ traits. For S species with abundances x_i , the deterministic Lotka-Volterra equations on which our stochastic model is based are given by

$$\frac{dx_i}{dt} = \beta x_i \left(1 - \frac{1}{K} \sum_{j=1}^S \alpha(w_{ij}) x_j \right), \tag{1}$$

where β is the intrinsic growth rate and K is the carrying capacity of each species. We take β and K to be species independent in our stochastic implementation of the Lotka-Volterra competition model to allow us to focus on the effects of niche differences rather than competitive asymmetries that would be present if K varied across species.

Each species has an associated trait value $u_i \in [0, 1]$ that is assumed to be related to species interactions with regulating factors. The function $\alpha(w_{ij})$ in Eq. 1 gives the strength of competition between two species i and j , which are at distance w_{ij} from each other on the “niche axis” or trait axis. Using a finite circular niche axis, we define the distance to be

$$w_{ij} := \min\{|u_i - u_j|, 1 - |u_i - u_j|\}. \tag{2}$$

We use a circular niche axis to prevent species near the edges from being more highly abundant due to the advantage of having fewer competitors. The circular niche axis could, for example, represent the case in which the actual range of traits extends beyond the range being considered. The form of the competition coefficients $\alpha(w_{ij})$ determines the type of dynamics. For niche dynamics,

$$\alpha(w_{ij}) = \exp\left[-\left(\frac{w_{ij}}{\sigma}\right)^\rho\right], \tag{3}$$

so that competition declines with increasing trait differences, and for neutral dynamics

$$\alpha(w_{ij}) = 1. \tag{4}$$

Our assumption that competition declines with increasing trait differences is based on the intuitive notion that traits drive ecological strategy, and the more similar species are in strategy, the more strongly they will compete. This property of competition also has empirical support (Johansson and Keddy 1991, Jiang et al. 2010, Burns and Strauss 2011). Larger values of ρ make the competition function more “box-like,” declining more slowly at first, and then falling off quickly when the trait differences reach σ (Appendix S1: Fig. S1). The model given by Eqs. 1 and 3 involves niche dynamics in that a suite of species can coexist stably and robustly (i.e., even under small parameter changes) on the trait axis only if they are far enough apart in trait values (as long as $\rho \geq 2$; MacArthur and Levins 1967, May 1973, Abrams 1983, Gyllenberg and Meszena 2005, Meszena et al. 2006, Szabo and Meszena 2006, Pigolotti et al. 2007, 2010, Barabas and Meszena 2009, Hernandez-Garcıa et al. 2009, Barabas et al. 2012, 2013a). The $\rho < 2$ case is biologically unrealistic, as continuity in species’ interactions with regulating factors would preclude it (Barabas et al. 2012, 2013a). This is because with $\rho < 2$, there is a kink, or corner in the competition coefficient function where trait difference is zero. If one considers competition as arising from resource use overlap, this kink can only arise when there is an unrealistic discontinuity in species resource utilization (e.g., a bird species could consume seeds of length 0.99999 cm, but not those of length 1 cm; Barabas et al. 2013a). Therefore, to simulate niche communities we use $\rho \geq 2$. The parameter σ is related to the width of species’ resource utilization ranges and determines the limiting trait difference between coexisting competitors (MacArthur and Levins 1967). Appendix S1 includes further discussion of the shape parameter ρ .

We use a stochastic implementation of the dynamics given by Eq. 1 with immigration added. The number of species S changes over time in our model due to immigration and extinction. In our stochastic model, recruitment, death, and immigration events can occur at any moment in time, each governed by species-specific probabilities per unit time that are representative of the dynamics in Eq. 1. Specifically, we assume that in any small time interval Δt , there are probabilities $b_i \Delta t$ and $d_i \Delta t$, that species i in the local community increases (through birth or immigration) or decreases by one individual, respectively, and a probability $s \Delta t$ that immigration of an individual of a species not currently in the local community occurs. We define the probabilities per unit time b_i , d_i , and s as

$$b_i = \beta x_i (1 - m) + \beta J m p_i \quad (\text{recruitment}), \tag{5}$$

$$d_i = \frac{\beta}{K} x_i \sum_{j=1}^S \alpha(w_{ij}) x_j \quad (\text{death}), \text{ and} \tag{6}$$

$$s = \beta J m \left(1 - \sum_{j=1}^S p_j \right) \quad (\text{immigration}), \tag{7}$$

where m is the proportion of new individuals being added to the community that are immigrants, p_i is the relative

abundance of species i in the regional pool, and J is the desired number of individuals in the local community. Note these expressions assume that the community is under viability selection, so deaths are density dependent while recruitment is density-independent. The rate b_i reflects the rate of both local births (first term) and arrival of new individuals through immigration (second term) for a species present in the local community. The death rate d_i is the density dependent portion of Eq. 1. We set these expressions up so that the total rate of new individuals being produced locally or entering the community through immigration ($\sum_i b_i + s$) is equal to βJ , and that the total immigration rate (the sum across species of the second term in b_i plus s) is equal to $m\beta J$, a fixed proportion of that total rate of new individuals entering the local community. These expressions also assume that the probability of an immigrating individual belonging to a given species is equal to its relative abundance in the regional pool, p_i . We take the relative abundances in the source pool to follow the Ewens sampling distribution with parameter θ (Etienne et al. 2007).

The continuous stochastic dynamics (Eqs. 5–7) can be simulated using the Gillespie algorithm (Gillespie 1977), in which one uses the relative rates of events to decide which event occurs next (e.g. the probability that the next event is an increase in abundance of species i is $b_i / (\sum_j (b_j + d_j) + s)$). The time that passes before the next event can be calculated by drawing from a distribution determined by the total event rate based on the current state of the community. In our Gillespie algorithm, when the event is chosen to be immigration of a species not present in the local community (Eq. 7), the species' trait value u_i is chosen at random. Then its relative abundance is chosen using the Ewens sampling formula and divided by the proportion of species in the regional pool that are not currently in the local community ($1 - \sum_{j=1}^S p_j$). This procedure is valid because the Ewens sampling formula applies to even a portion of an infinite neutral regional pool (Etienne et al. 2007). Note all events occur at a rate proportional to β , so its value only effects the amount of time between events (which we ignore, as we are focusing on the equilibrium communities).

Simulations were initiated with 250 species at equal abundance with randomly assigned trait values between 0 and 1, and were run for a large enough number of events that visual analysis suggested the average SAD across runs was near equilibrium. We plotted the average SAD across simulations at intermediate time points to determine the appropriate number of events. We ran the niche simulations for 5×10^7 events and the neutral simulations for 1×10^7 events. The SAD may continue to change subtly in the niche case beyond this, but the change is toward greater difference from the neutral SAD. To relate the SAD predictions of the model to familiar neutral SAD predictions, we set J to the size of the tree community in the 50-ha CTFS-ForestGEO plot on Barro Colorado Island (21,455 individuals >10 cm dbh in 1995; Hubbell et al. 2005), and the immigration probability m and fundamental biodiversity number θ to values under which neutral theory provides a good fit to the empirical species abundance distribution (0.098 and 47.8 respectively; Etienne 2005). Note that the total community size in our model is controlled by a combination of J and K .

In the neutral case, we can set both equal to the desired community size, but in the niche case, we tune K to achieve a target stationary community of approximately 21,455 individuals.

We modeled a variety of scenarios to isolate the role of different aspects of the interaction structure on the pattern of relative abundances across trait values and on the SAD it produces. We describe these scenarios in *Results*, as they build from basic outcomes of our model.

Simulations were performed using MATLAB (MathWorks, Natick, MA, USA) and required over 20,000 h of computation time, which was carried out on the Extreme Science and Engineering Discovery Environment (XSEDE), and on HPC resources at the University of Michigan and Tulane University. The code we used for our simulations is available in the Supplementary Material.

RESULTS

Emergent niche structuring

The neutral case ($\alpha(w_{ij}) = 1$) shows no distinct pattern of abundances along the trait axis (Fig. 1a). Under niche dynamics however, the model produces clumps of densely packed and abundant species, separated by regions with fewer and less abundant species as shown by the example with $\rho = 4$ and $\sigma = 0.15$ in Fig. 1b. As stated in *Introduction*, this model produces a clumping pattern that was mentioned briefly by Barabás et al. (2013a). The pattern is similar to that pointed out by Scheffer and van Nes (2006) but is maintained by immigration rather than the addition of intraspecific negative density dependence. The number of clumps is equal to the number of stably coexisting species that would be expected at equilibrium in the deterministic version of our model (Eq. 1), which numerical exploration shows is determined primarily by σ . We call the clumping pattern in our model “emergent niches” to emphasize that groups form as a result of the dynamics rather than being prescribed ahead of time, and that those groups are organized around equally spaced positions on the trait axis that would allow for stable coexistence in the deterministic model. At the end of each simulation, we can interpret the emerged clumps as occupying their own niches, or equally sized regions of the trait axis. We describe how we designate niche regions in *Further exploration: The importance of heterogeneity in interactions across niches*, where we consider “within-niche” and “between-niche” interactions. The number of clumps and hence niches that emerge can be tuned by choosing σ appropriately. Due to the circular niche axis and the fact that species interactions depend only on distance and not the absolute positions along the niche axis, only the relative positions of the clumps are determined by σ , with the exact locations varying through time and across simulations.

Varying ρ produces a range of competition functions that decline with increasing trait differences (Appendix S1: Fig. S1). There is no discernable niche structure with Gaussian ($\rho = 2$) competition coefficients (Appendix S1: Fig. S2). This is likely because of tight packing behavior (i.e., stable coexistence of a set of species arbitrarily close to each other on the trait axis) that can be generated by the deterministic

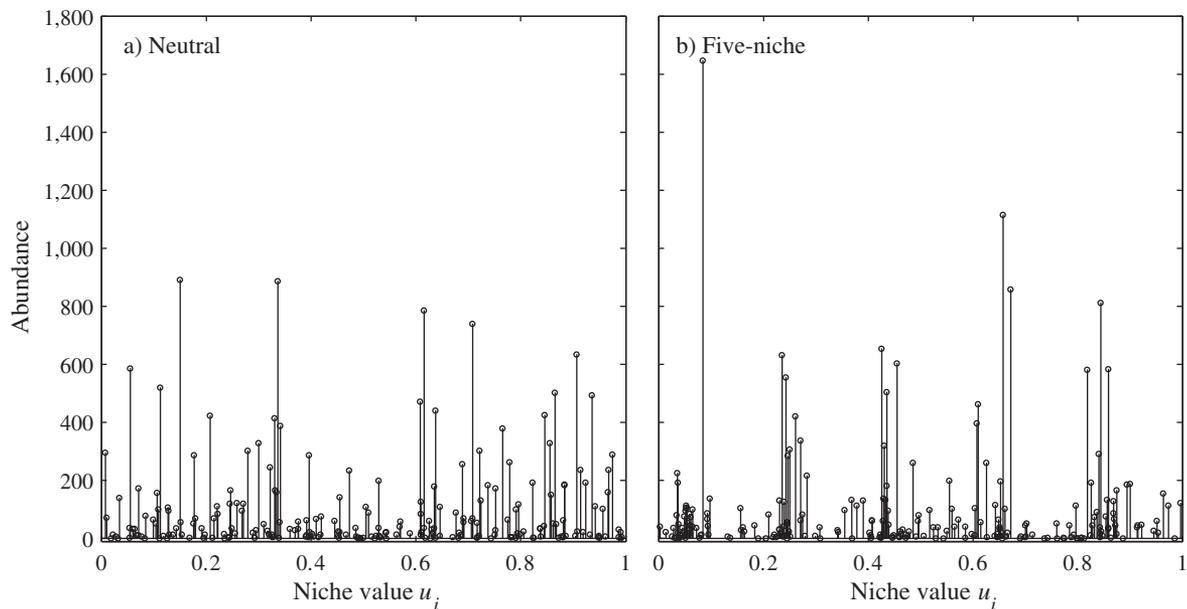


FIG. 1. Emergent niche structuring. Example (a) neutral and (b) five-niche configurations at the ends of the simulations, showing the abundances of all species in the community organized by trait value. (a) No pattern is visible along the trait axis in the neutral case. Carrying capacity $K = 21,455$; run length, 1×10^7 events; total abundance for this example, 21,235. (b) Clumping of abundant species is visible along the trait axis. Carrying capacity $K = 5410$, niche width parameter $\sigma = 0.15$, competition coefficient shape parameter $\rho = 4$; run length, 5×10^7 events; total abundance for this example, 21,346.

model in that case. Tight packing behavior is sensitive to parameter values (i.e., it is not robust, breaking down to limiting similarity with small variation in carrying capacity on the trait axis) (Roughgarden 1979, Gyllenberg and Meszena 2005, Meszena et al. 2006, Barabas et al. 2012). To avoid these special behaviors, we focus on the $\rho = 4$ case, as it is a conservative choice that yields representative niche structuring from this model (Fig. 1b, Appendix S1: Fig. S3). For more information regarding model assumptions and behavior related to variation in ρ , see Appendix S1.

Species abundance distributions

When niches are few relative to the number of species, the extreme niche model of Chisholm and Pacala (2010) (the CP model) produces SADs indistinguishable from the neutral case. To see if this was the case in our model, we first chose $\sigma = 0.15$ to allow for only five niches (Fig. 1b). The resulting 5-niche communities had an average richness of 233 species, and neutral communities had an average richness of 225 species. We then also considered abundance patterns with 20 and 50 niches ($\sigma = 0.037$ and 0.015 , respectively).

Our resulting 5-, 20-, and 50-niche communities had average SADs that differ more substantially from the neutral SAD than the SADs predicted by the CP model. In particular, with even just five niches, differences between the niche and neutral SADs averaged over 1,000 simulations are apparent (Fig. 2a). Because we used such a large number of simulations, the 95% confidence intervals of the mean number of species in each bin are so small they are difficult to distinguish, so they are not included in the SAD plots. The niche communities exhibit a strong central peak in the average SAD compared to the average neutral SAD. This involves both a higher proportion of species of medium

abundance (sixth to eighth abundance abundance classes on the Preston-style SAD plot shown) than the neutral case, and lower proportions of intermediately rare and intermediately high abundance species (third to fifth and ninth to tenth abundance classes, respectively). Our niche communities also exhibit large relative differences from the neutral case in the two highest abundance classes (i.e., relative to the number of species the neutral model predicts in those classes; Appendix S1: Fig. S5). The CP model prediction for the five-niche case is virtually indistinguishable from the neutral case (Fig. 2a) and does not feature the strong central peak. It does, however, have slightly fewer species than the neutral SAD in the two highest abundance classes, which is in contrast to the larger numbers of species in these classes produced by our model (Fig. 2a, Appendix S1: Fig. S5).

For a larger number of niches (20 and 50), the differences from the neutral case are still more substantial than predicted by the CP model (Fig. 2b,c). The predictions from our model and the CP model are very close in the large abundance classes, with the directions of differences from neutrality in those classes being the same in both models. However, our resulting average SAD also differs strongly from the neutral case along the rest of the curve while the CP prediction does not (Fig. 2, Appendix S1: Fig. S5). In particular, it still generates a higher proportion of species of medium abundance (sixth to eighth abundance abundance classes) and lower proportion of intermediately rare species (third to fifth abundance abundance classes) than seen in the neutral case.

Further exploration: The importance of heterogeneity in interactions across niches

The strength of interactions in our model with niche dynamics is determined by the distance in trait value

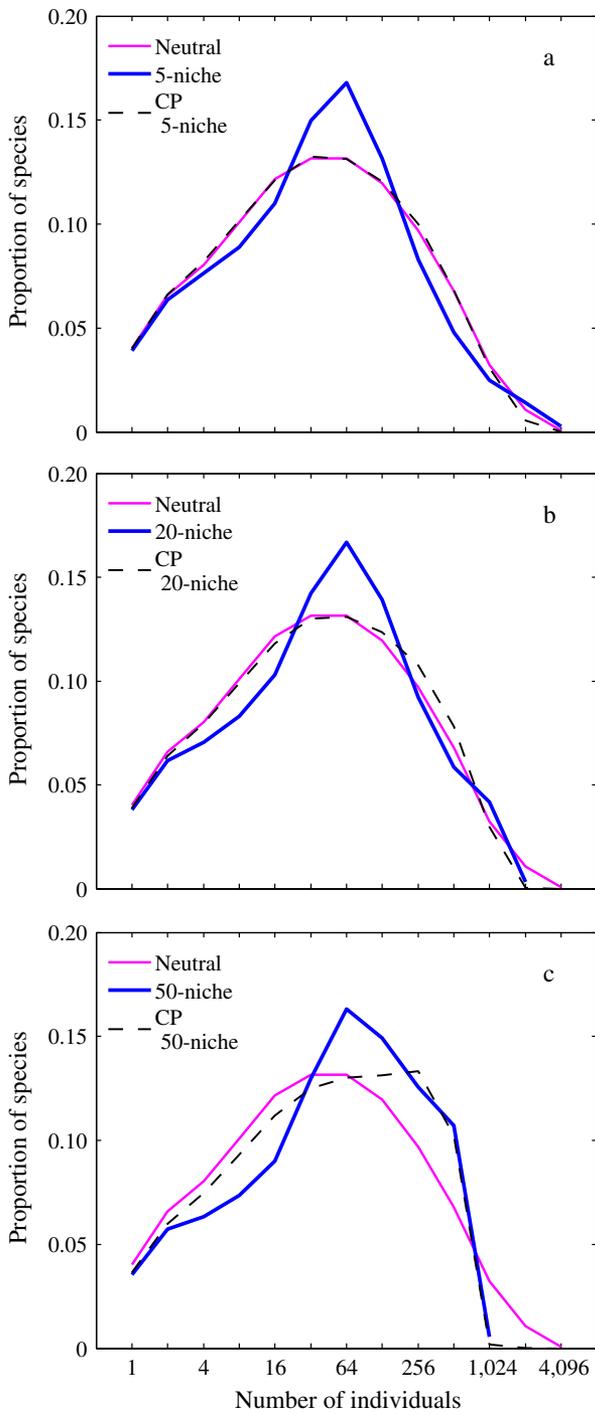


FIG. 2. Species abundance distributions (SADs) resulting from the neutral model, our niche model, and Chisholm and Pacala's (CP) niche model. In all SAD figures in this paper, SADs are shown in a Preston-style plot of the proportion of species in up to 12 logarithmically scaled abundance classes (Volkov et al. 2003). Our niche and neutral SADs are averaged over 1,000 simulations each, and the CP SAD is produced using the analytical formula in Chisholm and Pacala (2010). All neutral simulations use $K = 21,455$. All niche simulations use $\rho = 4$. (a) Five-niche communities ($K = 5410$, $\sigma = 0.15$), (b) 20-niche communities ($K = 1310$, $\sigma = 0.037$), and (c) 50-niche communities ($K = 519$, $\sigma = 0.015$). Mean species richness was 225, 232, 236, and 247 in the neutral, 5-, 20-, and 50-niche simulation communities respectively. Note that the x-axis is on a \log_2 scale.

between species regardless of the niche in which they fall, resulting in some key differences from the CP model. First, in our model, species in different niches, or clumps, compete with one another (i.e., there are “between-niche” interactions), whereas Chisholm and Pacala include only interactions within niches. Second, our model includes heterogeneity in (1) the strength of competition between species in different niches (“between-niche” interactions) and in (2) the strength of competition between species in the same niche (“within-niche” interactions), in contrast to the neutrality imposed within niches by Chisholm and Pacala. Both of these types of interaction heterogeneity have the same underlying source in our model, namely the dependence of competition on trait differences, but after niche structure emerges, within and between-niche interactions can be delineated.

To illustrate the influence of each of these differences between our model and the CP model, we simulated a variety of scenarios in which the interaction structure is effectively simplified in different ways. Due to the extensive computational resources required to run this large number of simulations, we focused only on the five-niche case for this analysis. First, to consider a case of our model with dynamics as similar as possible to the model of Chisholm and Pacala, we used niche dynamics (Eq. 3) and we restricted the possible trait values to the discrete set $\{0.1, 0.3, 0.5, 0.7, 0.9\}$. By doing this, each species falls into one of five niches in such a way that all species interact neutrally within a niche, as in the CP model (i.e., for i, j in the same niche, $\alpha(w_{ij}) = \alpha(0) = 1$). We also set $\rho = 100$. This makes our competition coefficients go sharply to 0 for species that differ by more than $\sigma = 0.15$ (see Appendix S1: Fig. S1, and note that even larger values of ρ result in a similar shape for the competition coefficients), and hence eliminates competition between species in different niches, as the CP model does. This case of our model and the CP model are essentially the same, with the small differences being that our model includes community-level density dependence while the CP model uses zero-sum dynamics, and that the CP model incorporates niche structure in the metacommunity while our model does not. We also do not constrain total niche abundances to be equal as is done in the CP model.

Second, we considered a case of our model that has neutral interactions within niches, but allows for interactions (with no heterogeneity) between niches. In implementation, this scenario differs from the previously described case only in that it uses $\rho = 4$ instead of $\rho = 100$, so that the competition strength falls less steeply with increasing trait difference.

Third, we illustrate the role of interaction heterogeneity in shaping the SAD by exploring two intermediate cases between the above scenarios and full niche dynamics. We set up the cases with intermediate heterogeneity by choosing each species' trait value from five equally spaced regions of the trait axis (instead of five discrete values). A wider region produces greater heterogeneity in competitive effects because it increases the range of possible values for w_{ij} . In the first intermediate case, we took the niche regions to be of widths 0.05 and 0.1 (i.e. 1/4 and 1/2 of the full niche width 0.2). Appendix S1: Fig. S6 shows example final configurations of these simulations, which help illustrate the trait spans used.

Finally, we simulated two additional cases of our model to explore the specific roles of heterogeneity in “between-niche” interactions, and heterogeneity in “within-niche” interactions. Both of these cases were initiated from the final communities of the full five-niche simulations so that niches were already present and we could distinguish between within- and between-niche interactions. In the case with only between-niche interaction heterogeneity, interactions between species in different niches depend on trait difference, and interactions within niches are neutral ($\alpha(w_{ij})$ is given by Eq. 3 if species i and j are in separate niches and is constant otherwise), and vice-versa in the “within-niche” heterogeneity case. We delineated species’ niches according to the abundance structure in the final five-niche configurations, where abundances tend to be highest at the centers of the niches. For each simulation, we identified the first niche by designating the trait of the most abundant species to be at the center of that niche. We then designated the remaining niche centers to be equally spaced across the niche axis with the first. Each niche occupies a region of width 0.2. For each case, we ran 1,000 simulations each for 5×10^5 events.

Analyzing the output of these simulations leads to a number of insights. Fig. 3a shows the SADs for the neutral model, the CP model prediction, and the two simplest cases of our model we considered, namely the case analogous to the CP model, and the case with homogenous between-niche interactions added to our analogue of the CP model. We see that these simple cases of our model produce SADs very similar to one another, and to the CP model prediction, though with a slightly greater deviation from the neutral SAD (Fig. 3a). This suggests that the presence of homogeneous between-niche interactions do not play much of a role in shaping the SAD of our full model, and neither do the

differences in the assumptions behind the CP model prediction and our analogous version of the CP model (i.e., our model includes community-level density dependence while the CP model uses zero-sum dynamics, and the CP model incorporates niche structure in the metacommunity and constrains niche abundances to be equal while our model does neither).

Fig. 3b shows the SADs for our cases of intermediate levels of interaction heterogeneity, along with the neutral and full niche dynamics cases. (Note that a trait span of 0 corresponds to our analog of the CP model with homogeneous between-niche interactions added.) Increasing interaction heterogeneity (by increasing the width of the niche regions) brings the SAD closer to the SAD of our full model. Furthermore, Fig. 3b shows that the SAD from the model with half-sized niche regions is very similar to the SAD of our full model.

Within-niche interaction heterogeneity leads to higher species abundances toward the edges of a niche, which is the opposite pattern of species abundances in a niche from our full model (Fig. 4a). This is not surprising since species near the centers of the initial niches will be subject to the most competition from other species sharing that niche, while species near the edge will be subject to the least. The reverse is true when considering the strength of between-niche competition, which will be at a minimum for species at the center of the niche. Hence these patterns of relative abundance within the niche illustrate the dominant influence of heterogeneity in between-niche interactions. This viewpoint is further supported by Appendix S1: Fig. S8, which shows the strength of between-niche and within-niche competition as a function of position within the niche under the emergent niche structure from our model.

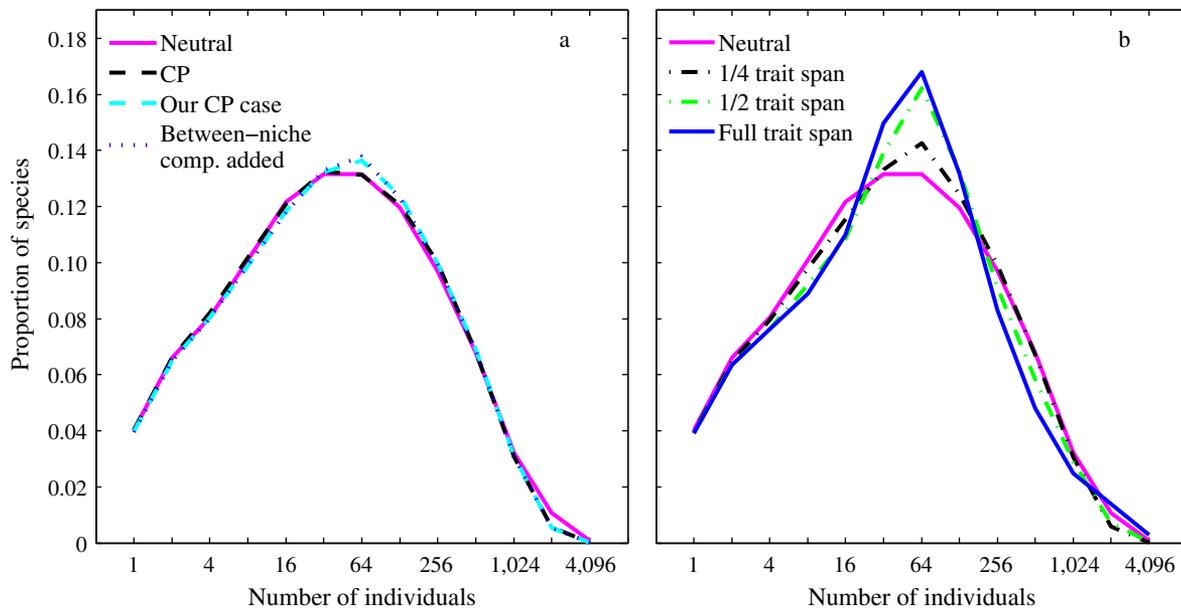


FIG. 3. Effects of homogeneous between-niche interactions and interaction heterogeneity on SADs. (a) SADs for the neutral model, the CP niche model, and two variations of our niche model: an analog of the CP model (Our CP case, $\rho = 100$, $K = 4660$), and the CP analog with homogeneous between-niche competition added (Between-niche comp. added, $\rho = 4$, $K = 4300$). (b) SADs for the neutral case, our regular niche model case with full interaction heterogeneity (Full trait span), and two cases with intermediate levels of interaction heterogeneity: 1/4 trait span and 1/2 trait span. In the latter two cases, species trait values are chosen from equally spaced regions on the trait axis sized as 1/4 or 1/2 of a niche width (0.2) respectively, and $K = 4,830$ and $K = 5,084$ respectively. Note that x-axes are on a log₂ scale.

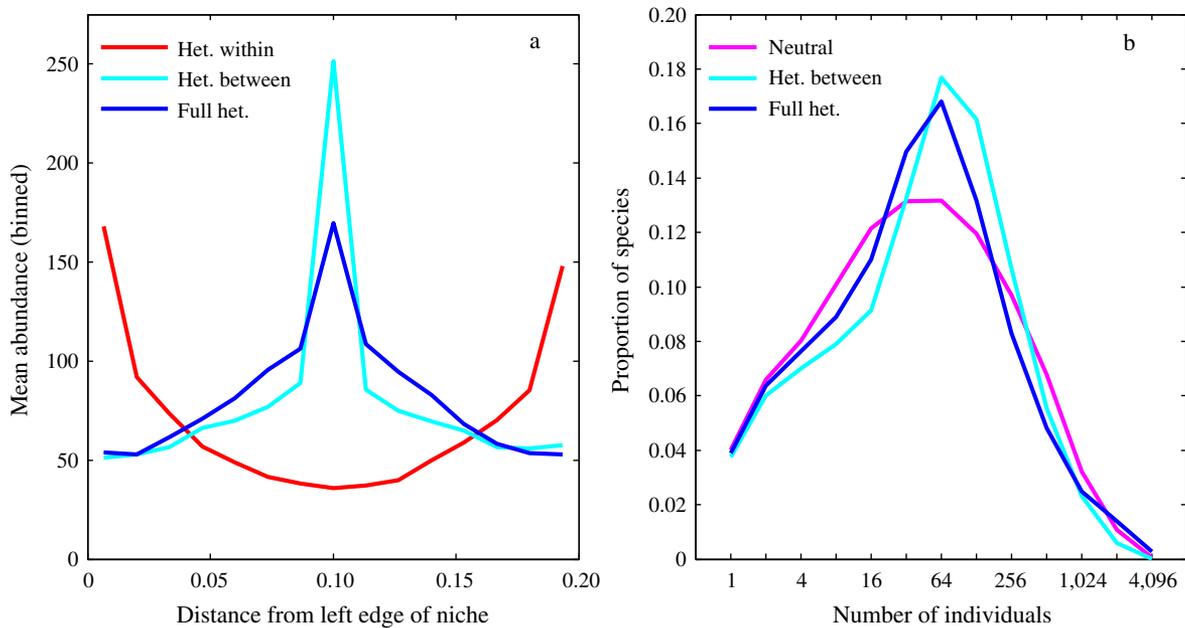


FIG. 4. Effects of between-niche and within-niche interaction heterogeneity on SADs in the five-niche case. (a) Binned abundances in a single niche with bins averaged over 1,000 simulations. “Het. between” has heterogeneity in between-niche interactions only; “Het. within” has interaction heterogeneity within niches only ($\alpha = 1$ for between-niche interactions), and “Full het.” is our full model. (b) SADs averaged over 1,000 simulations. Note that the x -axis is on a \log_2 scale.

We also find that heterogeneity in within-niche competition is playing an important role. The decline in species abundance with distance from the center of the niche in Fig. 4a is steeper in the between-niche interaction heterogeneity case than in the full interaction heterogeneity case (i.e., our original niche dynamics model). Heterogeneity in within-niche interactions is counteracting the degree of dominance of species at the center of the niche that would otherwise result.

In Fig. 4b we see further evidence for the influence of between-niche interaction heterogeneity and the counteracting influence of within-niche interaction heterogeneity. The SAD for the case with between-niche interaction heterogeneity essentially differs from the neutral model SAD in similar ways to our full model, but to a larger degree, with the exception of the largest abundance class. For greater readability, we do not plot the within-niche heterogeneity case SAD in Fig. 4b. As stated above and shown in Fig. 4a, it produces the wrong trend of abundance with trait values within niches, and in this sense, is a poor approximation to our full model.

DISCUSSION

To determine whether observed SADs can be used to infer community assembly processes, we first need to know how they change with the presence of niche dynamics. Purves et al. (2005) and Chisholm and Pacala (2010) recently argued that niche and neutral SADs are very similar when there are many species per niche, and in fact identical in the infinite diversity limit. They demonstrated this analytically for the case of discrete, non-interacting niches with neutral dynamics within each niche. Here we have shown that SADs

show distinct differences between niche and neutral communities when niche structuring emerges from the dynamics of a model with trait-dependent competition instead of being modeled in a simplified rigid manner. In particular, visually apparent differences arise in the SAD even with a small number of niches relative to the number of species. Furthermore, we have shown that the heterogeneity in interaction strength produced by trait-dependent competition strongly influences the shape of the SAD, and we illustrated how heterogeneity in between-niche and within-niche interactions each contribute to that influence.

It is clear from our study that the presence of niches in a community of competing species can influence the shape of the SAD, and that while the extreme niche structuring of the CP model makes it feasible to derive valuable analytical results, it is too extreme to reflect processes that may give rise to differences from a neutral SAD. This perhaps should not be surprising given that the rigid niche structure of the CP model could more readily be interpreted as a set of disparate groups of organisms such as phytoplankton put together with a group of trees in a rainforest and a collection of island birds, etc., than niches in a community of interacting species. Indeed, Haegeman et al. (2011) point out that a model of independent, unregulated species gives the same SAD predictions as a zero-sum neutral model for all levels of diversity, and hence that it is not surprising that extreme niche structuring leads to the same distributions as a neutral model in the high diversity limit. When there are more species than niches, species in separate niches would likely instead retain some level of interaction, with heterogeneity in the intensity of those interactions due to variation in similarity of resource use or other competitive factors with the dominant species in a nearby niche. In our model, where

niche structure emerges from competition that depends on species trait differences, species organize into niches in such a way that there are significant interactions across niches, and the heterogeneity in those interactions shapes species' relative abundances.

We highlighted that heterogeneous interactions across niches are dominant in shaping the pattern of species abundances along the trait axis. To demonstrate this, we used five-niche communities, though further investigation would be needed to generalize these results. While understanding exactly how heterogeneous interactions within or between niches affect differences in particular abundance classes is not intuitive, we showed how within and between-niche interactions each contribute to shaping abundances on the trait axis by looking at the communities that arise in each case separately. The heterogeneous interactions within the niche appear to buffer the advantage that species at the centers of niches would otherwise have based only on between-niche interactions, and their inclusion results in an SAD that is generally less exaggerated than that of communities with between-niche heterogeneity alone. In particular, communities with between-niche heterogeneity alone have a sharper central peak in their SAD than our full model. Appendix S2 includes further discussion of the influence of interaction heterogeneity on particular SAD bins.

Our model relaxes the strict assumptions in the CP model that produce neutral-like results unless there is a very high number of niches. A couple of recent studies have considered perhaps more subtle but still important relaxations of the extreme niche structure of Chisholm and Pacala (2010), and have also shown increased differences between SADs of neutral and niche structured communities, even for a small number of niches. Walker (2007) showed that when niches differed in their diversity, differences were produced in SADs, even in the high diversity limit. Bewick et al. (2015) recently considered a modification in which species can have membership in multiple niches, but interactions within niches are still neutral. Their model produced a surplus of rare species compared to the neutral case, even with a small number of niches. This effect was seemingly due to variation across species in niche breadth (i.e., the number of niches each can occupy) incorporated in their model, as the species with narrow niche breadths tended to be rare.

Although our model captures a key feature of competition that can lead to the emergence of niches, namely dependence of interactions on trait differences, further empirical inquiry into the actual competitive interaction structure found in communities is needed in order to better resolve the differences from neutral SADs that would be expected. Beyond the decline of competition with increasing trait differences, empirical knowledge of competition coefficients is limited, and a variety of specific functional forms have been proposed to model different situations (Abrams 1975).

A specific type of additional complexity that may be important in many systems is the presence of hierarchical interactions (e.g., Harpole and Tilman 2006; Kunstler et al. 2012), which could introduce a dependence of competition strength on the trait itself and not just trait differences. Chave et al. (2002) studied the influence of such niche dynamics on the SAD. Although their study focused on the range of SAD patterns predicted as dispersal parameters

varied, they also mentioned differences found for fixed parameter values (and significant niche structure) that involved an increase in the number of species of moderate abundance like that observed here. Their hierarchical competition model, however, involved unrealistic discontinuities (Barabás et al. 2013a, D'Andrea et al. 2013). Another aspect of complexity in competitive interactions worthy of consideration is the potential for the decrease in competition with increasing trait differences to be non-monotonic, which can occur when competition is through consumption of populations that can be driven extinct (Abrams et al. 2008). Further study is needed to more fully understand how underlying dynamics affect the shape of a community's SAD.

Our analysis has shown that niche structuring emerging from competition dependent on trait differences can *in principle* influence SAD patterning even with high diversity and a small number of niches. Future studies may determine whether it will typically have such an influence, and further, whether its influence is actually detectable in data (as Al Hammal et al. [2015] have considered for the model of Pigoletti and Cencini [2013]). Factors that should be considered include the shape of the competition function, the breakdown of population growth rates into birth and death rates, the immigration rate, and the metacommunity species abundance distribution. The role of "fitness differences" (Chesson 2000) should also be considered, as recent studies in the context of enforced niche structure have found that they can counteract the effects of niche differences or "stabilization" on the SAD (Du et al. 2011, Carroll and Nisbet 2015). Coupling study of these factors in the context of a model like that studied here, with study of an array of more biologically detailed and empirically ground-truthed system-specific competition models may help place communities found in nature within the larger spectrum of models that can be mathematically constructed. Consideration of the impact of niche structure on community metrics containing more information than SADs may also prove worthwhile (Pigoletti and Cencini 2013, Tang and Zhou 2013, Carroll and Nisbet 2015).

ACKNOWLEDGMENTS

This material is based upon work supported by the National Science Foundation under grant no. 1038678, "Niche versus neutral structure in populations and communities," funded by the Advancing Theory in Biology program. This work used the Extreme Science and Engineering Discovery Environment (XSEDE), which is supported by National Science Foundation grant number OCI-1053575. We thank Veronica Vergara for assistance with running MATLAB on the Condor Pool, which was made possible through the XSEDE Extended Collaborative Support Service (ECSS) program. This work also used HPC resources at the University of Michigan, and at Tulane University with support from the Tulane Center for Computational Science. We also thank the anonymous reviewers whose constructive suggestions helped improve this manuscript.

LITERATURE CITED

- Abrams, P. 1975. Limiting similarity and the form of the competition coefficient. *Theoretical Population Biology* 8:356–375.
 Abrams, P. 1983. The theory of limiting similarity. *Annual Review of Ecology and Systematics* 14:359–376.

- Abrams, P. A., C. Rueffler, and R. Dinnage. 2008. Competition-similarity relationships and the nonlinearity of competitive effects in consumer-resource systems. *American Naturalist* 172:463–474.
- Al Hammal, O., D. Alonso, R. S. Etienne, and S. J. Cornell. 2015. When can species abundance data reveal non-neutrality? *PLoS Computational Biology* 11. <https://doi.org/10.1371/journal.pcbi.1004134>
- Barabás, G., and G. Meszéna. 2009. When the exception becomes the rule: the disappearance of limiting similarity in the Lotka-Volterra model. *Journal of Theoretical Biology* 258:89–94.
- Barabás, G., S. Pigolotti, M. Gyllenberg, U. Dieckmann, and G. Meszéna. 2012. Continuous coexistence or discrete species? A new review of an old question. *Evolutionary Ecology Research* 14:523–554.
- Barabás, G., R. D'Andrea, and A. M. Ostling. 2013a. Species packing in nonsmooth competition models. *Theoretical Ecology* 6:1–19.
- Barabás, G., R. D'Andrea, R. Rael, G. Meszéna, and A. Ostling. 2013b. Emergent neutrality or hidden niches? *Oikos* 122:1564–1571.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- Bewick, S., R. A. Chisholm, E. Akçay and W. Godsoe. 2015. A stochastic biodiversity model with overlapping niche structure. *Theoretical Ecology* 8:81–109.
- Bonsall, M. B., V. A. Jansen, and M. P. Hassell. 2004. Life history trade-offs assemble ecological guilds. *Science* 306:111–114.
- Burns, J. H., and S. Y. Strauss. 2011. More closely related species are more ecologically similar in an experimental test. *Proceedings of the National Academy of Sciences USA* 108:5302–5307.
- Carroll, I. T., and R. M. Nisbet. 2015. Departures from neutrality induced by niche and relative fitness differences. *Theoretical Ecology* 8:449–465.
- Chase, J. M., and M. A. Leibold. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois, USA.
- Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* 159:1–23.
- Chesson, P. 1991. A need for niches? *Trends in Ecology & Evolution* 6:26–28.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Chisholm, R. A., and S. W. Pacala. 2010. Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proceedings of the National Academy of Science USA* 107:15821–15825.
- Clark, J. S., M. Silman, R. Kern, E. Macklin and J. Hille Ris Lambers. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology* 80:1475–1494.
- D'Andrea, R., and A. Ostling. 2016. Challenges in linking trait patterns to niche differentiation. *Oikos* 125:1369–1385.
- D'Andrea, R., G. Barabás, and A. Ostling. 2013. Revising the tolerance-fecundity trade-off; or, on the consequences of discontinuous resource use for limiting similarity, species diversity, and trait dispersion. *American Naturalist* 181:E91–E101.
- Du, X., S. Zhou, and R. S. Etienne. 2011. Negative density dependence can offset the effect of species competitive asymmetry: a niche-based mechanism for neutral-like patterns. *Journal of Theoretical Biology* 278:127–134.
- Ernebjerg, M., and R. Kishony. 2011. Dynamic phenotypic clustering in noisy ecosystems. *PLoS Computational Biology* 7:e1002017.
- Etienne, R. S. 2005. A new sampling formula for neutral biodiversity. *Ecology Letters* 8:253–260.
- Etienne, R. S., D. Alonso, and A. J. McKane. 2007. The zero-sum assumption in neutral biodiversity theory. *Journal of Theoretical Biology* 248:522–536.
- Gillespie, D. T. 1977. Exact stochastic simulation of coupled chemical reactions. *Journal of Physical Chemistry* 81:2340–2361.
- Gyllenberg, M., and G. Meszéna. 2005. On the impossibility of coexistence of infinitely many strategies. *Journal of Mathematical Biology* 50:133–160.
- Haegeman, B., and M. Loreau. 2011. A mathematical synthesis of niche and neutral theories in community ecology. *Journal of Theoretical Biology* 269:150–165.
- Haegeman, B., and R. S. Etienne. 2011. Independent species in independent niches behave neutrally. *Oikos* 120:961.
- Hardin, G. 1960. The competitive exclusion principle. *Science* 131:1292–1297.
- Harpole, W. S., and D. Tilman. 2006. Non-neutral patterns of species abundance in grassland communities. *Ecology Letters* 9:15–23.
- Hernández-García, E., C. López, S. Pigolotti and K. H. Andersen. 2009. Species competition: coexistence, exclusion and clustering. *Philosophical Transactions of the Royal Society A* 367:3183–3195.
- Holt, R. D. 2006. Emergent neutrality. *Trends in Ecology & Evolution* 21:531–533.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*, Volume 32. Princeton University Press, Princeton, New Jersey, USA.
- Hubbell, S. P., R. Condit and R. B. Foster. 2005. Barro Colorado Forest census plot data. <https://ctfs.arnarb.harvard.edu/webatlas/datasets/bci>
- Jiang, L., J. Tan, and Z. Pu. 2010. An experimental test of darwins naturalization hypothesis. *American Naturalist* 175:415–423.
- Johansson, M. E., and P. A. Keddy. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity: an experimental study on two guilds of wetland plants. *Oikos* 60:27–34.
- Kohyama, T. 1993. Size-structured tree populations in gap-dynamic forest—the forest architecture hypothesis for the stable coexistence of species. *Journal of Ecology* 81:131–143.
- Kunstler, G., S. Lavergne, B. Courbaud, W. Thuiller, G. Vieilledent, N. E. Zimmermann, J. Kattge, and D. A. Coomes. 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters* 15:831–840.
- Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371–1382.
- Leibold, M. A., et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* 104:413–423.
- MacArthur, R., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. *American Naturalist* 101:377–385.
- May, R. M. 1973. *Stability and complexity in model ecosystems*, Volume 1. Princeton University Press, Princeton, New Jersey, USA.
- Meszéna, G., M. Gyllenberg, L. Pa'sztor, and J. A. Metz. 2006. Competitive exclusion and limiting similarity: a unified theory. *Theoretical Population Biology* 69:68–87.
- Mouquet, N., and M. Loreau. 2003. Community patterns in source-sink metacommunities. *American Naturalist* 162:544–557.
- Muller-Landau, H. C. 2001. *Seed dispersal in a tropical forest: empirical patterns, their origins, and their consequences for community dynamics*. Thesis. Princeton University, Princeton, New Jersey, USA.
- Nekola, J. C., and J. H. Brown. 2007. The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecology Letters* 10:188–196.
- Pigolotti, S., and M. Cencini. 2013. Species abundances and lifetimes: From neutral to niche-stabilized communities. *Journal of Theoretical Biology* 338:1–8.
- Pigolotti, S., C. López, and E. Hernández-García. 2007. Species clustering in competitive Lotka-Volterra models. *Physical Review Letters* 98:258101.
- Pigolotti, S., C. López, E. Hernández-García, and K. H. Andersen. 2010. How Gaussian competition leads to lumpy or uniform species distributions. *Theoretical Ecology* 3:89–96.

- Purves, D. W., and S. W. Pacala. 2005. Ecological drift in niche-structured communities: neutral pattern does not imply neutral process. Pages 107–138 in D. Burslem, M. Pinard, and S. Hartley, editors. *Biotic interactions in the tropics: their role in the maintenance of species diversity*. Cambridge University Press, Cambridge, UK.
- Roughgarden, J. 1979. *Theory of population genetics and evolutionary ecology*. Macmillan, New York, New York, USA.
- Scheffer, M., and E. H. van Nes. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. *Proceedings of the National Academy of Sciences USA* 103:6230–6235.
- Segura, A. M., D. Calliari, C. Kruk, D. Conde, S. Bonilla, and H. Fort. 2011. Emergent neutrality drives phytoplankton species coexistence. *Proceedings of the Royal Society B* 278:2355–2361.
- Segura, A., C. Kruk, D. Calliari, F. García-Rodríguez, D. Conde, C. Widdicombe, and H. Fort. 2013. Competition drives clumpy species coexistence in estuarine phytoplankton. *Scientific Reports* 3:1037.
- Silvertown, J. 2004. Plant coexistence and the niche. *Trends in Ecology & Evolution* 19:605–611.
- Szabó, P., and G. Meszéná. 2006. Limiting similarity revisited. *Oikos* 112:612–619.
- Tang, J., and S. Zhou. 2013. Hybrid niche-neutral models outperform an otherwise equivalent neutral model for fitting coral reef data. *Journal of Theoretical Biology* 317:212–218.
- Vernon, R., N. K. Dulvy, and R. P. Freckleton. 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. *Ecology Letters* 12:1079–1090.
- Vernon, R., E. H. van Nes, and M. Scheffer. 2012. Emergent neutrality leads to multimodal species abundance distributions. *Nature Communications* 3:663.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424:1035–1037.
- Volkov, I., J. R. Banavar, F. He, S. P. Hubbell, and A. Maritan. 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438:658.
- Walker, S. C. 2007. When and why do non-neutral metacommunities appear neutral? *Theoretical Population Biology* 71:318–331.
- Yan, B., J. Zhang, Y. Liu, Z. Li, X. Huang, W. Yang, and A. Prinzing. 2012. Trait assembly of woody plants in communities across sub-alpine gradients: Identifying the role of limiting similarity. *Journal of Vegetation Science* 23:698–708.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2238/supinfo>