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1 Title: Emergent niche structuring leads to increased
2 differences from neutrality in species abundance
3 distributions

4 Running Head: Emergent niches and neutral SADs

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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.

Keywords: competition, coexistence, community assembly, Lotka–Volterra model,

38 neutral theory, trait axis,

39 **1 Introduction**

40 A question debated in community ecology is whether the pattern of species abundances in
41 a given community reflects underlying mechanisms involved in assembling it, or instead
42 reflects only broad mechanisms common not only across communities, but to a variety
43 of complex systems (Nekola and Brown 2007). Neutral theory (Bell 2000, Hubbell 2001)
44 and niche differentiation (Chase and Leibold 2003, Chesson 1991, 2000, Leibold 1995,
45 Meszena et al. 2006) provide different hypotheses for mechanisms that drive the patterns
46 of diversity and abundance we see in nature. The principle of competitive exclusion
47 says that species must be sufficiently different from each other with regard to traits
48 relevant to competition in order to coexist (Hardin 1960). Competitive exclusion can be
49 exemplified by Lotka-Volterra competition models, which predict that species that are
50 sufficiently different can coexist stably and can invade populations of other species from
51 low abundance (MacArthur and Levins 1967, May 1973). On the other hand, neutral
52 theory suggests that coexistence is more influenced by species' similarity rather than
53 their differences, with similarity allowing species to persist together for long periods of
54 time (Chesson 2000, Hubbell 2001). Neutral theory then posits that in any given local
55 community immigration maintains diversity by balancing extinction events that eventually
56 occur due to stochasticity (Hubbell 2001, Volkov et al. 2005). Even though the nature
57 of coexistence differs in communities with neutral versus niche dynamics, recent studies
58 have suggested that the species abundance distributions (SADs) of these two types of
59 communities are too similar to be used to infer the presence of niche structure (Chave
60 et al. 2002, Mouquet and Loreau 2003, Purves et al. 2005, Chisholm and Pacala 2010,
61 Haegeman and Loreau 2011, Pigolotti and Cencini 2013, Carroll and Nisbet 2015).

62 Many of the recent studies considering the differences between niche and neutral SADs

63 have mainly considered whether niche and neutral community assembly modes produce
64 SADs within the same range of forms as model parameters are varied (Chave et al. 2002,
65 Mouquet and Loreau 2003, Pigolotti and Cencini 2013). Neutral models in ecology consist
66 of immigration from a “metacommunity” source pool to a local community where the
67 SAD is determined by the number of species and the rates of speciation and dispersal
68 (Hubbell 2001). Speciation and dispersal rates in particular are difficult to measure and
69 are therefore treated as free parameters of the neutral model, which is fit to observations.
70 In this case, significant differences in the ranges of SADs that niche and neutral dynamics
71 yield might suggest that empirical SADs can give insight into the underlying processes
72 shaping the community. However, if speciation and dispersal rates could be estimated
73 using data, then more specific neutral SAD predictions could be made based on those
74 parameter values and compared with data. The relevant theoretical question for whether
75 observed SADs are useful for insight into underlying processes is then whether there
76 are differences between the particular niche and neutral SADs produced with the same
77 parameter values. In fact, information is becoming increasingly available on dispersal rates
78 (Clark et al. 1999, Muller-Landau 2001), as is data that could be used to approximate the
79 abundance distribution of the regional pool in a neutral model and estimate speciation
80 rate. For example, data is becoming available on the abundances of tree species in a large
81 region of the Panama basin surrounding Barro Colorado Island (Hubbell et al. 2005)
82 that might serve this purpose. Furthermore, if SADs were known to be more revealing
83 of underlying processes when parameters are measurable, this might motivate further
84 collection of dispersal and regional abundance data. Hence a comparison is warranted
85 between niche and neutral SADs with fixed dispersal and speciation parameters to see if
86 SADs might reveal the presence of non-neutral processes when parameters are known.

87 Some recent studies have considered differences between niche and neutral SADs
88 occurring for fixed speciation and immigration parameters. They conclude that a large
89 amount of niche structuring is needed to create substantial differences between niche

90 and neutral SADs. For example, Purves et al. (2005) and Chisholm and Pacala (2010)
91 considered a simplified, extreme niche structure in which species fall into discrete,
92 non-interacting guilds within which they interact neutrally. Chisholm and Pacala (2010)
93 showed that this type of stochastic niche model produces SADs that are virtually
94 indistinguishable from the neutral SAD when species richness is much higher than
95 the number of niches, and that it takes a large number of niches to obtain substantial
96 differences between niche and neutral cases. Haegeman and Loreau (2011) and Pigolotti
97 and Cencini (2013) came to the same conclusion when considering another type of
98 simplified niche structure in which intraspecific and interspecific competition were each
99 respectively determined by a single parameter. They found that SADs change little as
100 a small amount of niche structure is enforced by strengthening intraspecific relative to
101 interspecific competition.

102 However, it may be premature to draw conclusions about the community abundances
103 typically expected in nature from these studies, as real interaction structures are expected
104 to be more complex than the ones in the models described above. In particular, empirical
105 evidence supports trait distance as a key determiner of the strength of competition (Burns
106 and Strauss 2011, Jiang et al. 2010, Johansson and Keddy 1991). This is what one would
107 expect if there is an array of resources or “limiting factors” (Levin 1970, Mesz ena et al.
108 2006) for competing species to partition based on continuous trait values. For example,
109 water and nutrients available at different soil depths might be used differently across plant
110 species that differ in their root depth (Silvertown 2004). Available patches of different ages
111 since disturbance might be exploited differently across tree species that differ in their life
112 history strategies (Kohyama 1993). In these examples, species with similar traits should
113 compete more strongly because they will consume available resources or interact similarly
114 with “limiting factors.” Recent theoretical studies show that competitive interactions
115 driven by species differences along a trait axis typically lead to niche structuring in
116 the form of persistent clusters of similar species (Bonsall et al. 2004, Scheffer and van

117 Nes 2006, Holt 2006, Pigolotti et al. 2007, Segura et al. 2011, Ernebjerg and Kishony
118 2011, Vergnon et al. 2012, D'andrea and Ostling 2016). These clusters emerge from the
119 dynamics themselves instead of being externally imposed. The niche dynamics studied
120 by Purves et al. (2005) and Chisholm and Pacala (2010) could be viewed as a possible
121 limiting case of this expected structure, with identical competitors (neutral dynamics)
122 within clusters, but no interaction at all between clusters.

123 Here we consider SADs in a stochastic competition model in which structuring
124 of species into niches emerges rather than being imposed. Specifically, we consider a
125 stochastic version of the classic Lotka–Volterra competition model along a trait axis,
126 where interaction strength declines with interspecific trait difference, a simple model that
127 captures arguably the most salient feature of competition structuring many ecological
128 communities. This model predicts system-specific limits to the similarity of coexisting
129 species (MacArthur and Levins 1967, May 1973, Abrams 1983, Szabó and Meszéna 2006,
130 Barabás and Meszéna 2009, Barabás et al. 2012, 2013a). Perhaps counterintuitively, the
131 transient state of the Lotka-Volterra model involves emergent clustering of species on
132 the trait axis (the species nearest to those that coexist at equilibrium take the longest to
133 be excluded). The addition of intraspecific negative density dependence, environmental
134 fluctuations, or mutation typically make clustering created by competitive interactions
135 persistent. This “self-organized similarity” or “emergent neutrality” was highlighted in
136 a variety of recent studies (Bonsall et al. 2004, Scheffer and van Nes 2006, Holt 2006,
137 Vergnon et al. 2009, 2012, Segura et al. 2011, Ernebjerg and Kishony 2011), and reviewed
138 in D'andrea and Ostling (2016). Some recent studies have highlighted observed clumped
139 patterns of species on trait axes in support of those consistent with an emergent niche
140 perspective (Vergnon et al. 2009, Segura et al. 2013, Yan et al. 2012). We use a stochastic
141 version of the Lotka-Volterra model with immigration that produces a persistent pattern
142 of emergent clusters (Barabás et al. 2013b) through “mass effects” (Leibold et al. 2004),
143 whereby immigration counteracts competitive exclusion and produces higher average

144 abundances in species that would be excluded more slowly. These emergent clusters can be
145 viewed as separate “niches” in the sense that species at the centers of these clusters would
146 stably coexist with one another.

147 We use our model to consider the potential for niche dynamics to produce different
148 SADs than the neutral case when speciation and dispersal parameters are fixed. We also
149 compare differences from SADs produced by the extreme niche model of Chisholm and
150 Pacala (2010), which we will refer to as the C&P model throughout this paper. We also
151 demonstrate that the heterogeneity in interaction strength deriving from the dependence
152 of competition on trait differences in our model is shaping the SAD. We show that
153 heterogeneity in interactions between species in separate niches is important in driving the
154 observed species abundance patterns, even though between-niche interactions are weaker
155 than within-niche interactions. This study lays the groundwork for further investigations
156 on the distinguishability of niche and neutral assembly modes using SADs and other
157 community patterns when niches emerge rather than being imposed. Furthermore, it
158 highlights the necessity of understanding the competitive interactions and emergent niche
159 structures that occur in nature for continued development of a stochastic niche theory for
160 SADs and other community properties.

161 **2 Model and Simulation Methods**

162 We use the spatial structure often used in neutral models in ecology consisting of a
163 “metacommunity” pool of species that can immigrate into a smaller local community
164 (Hubbell 2001). We focus on the influence of niche differentiation on SADs only in the
165 local community. We do not incorporate niche differentiation into the source pool, or
166 model its dynamics explicitly. Instead we assume the relative abundances of species
167 in the source pool follow a Ewens sampling distribution, as would be expected for an
168 infinite metacommunity governed by the standard neutral model involving point speciation

169 (Etienne et al. 2007). We model immigration from this source pool as stochastic, and
 170 model the dynamics of the species in the local community as a stochastic implementation
 171 of the standard Lotka–Volterra competition differential equations, where the strength of
 172 competition is a function of the distance between competitors’ traits. For S species with
 173 abundances x_i , the deterministic Lotka-Volterra equations on which our stochastic model
 174 is based are given by

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

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

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

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

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

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

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

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

190 Our assumption that competition declines with increasing trait differences is based on
191 the intuitive notion that traits drive ecological strategy, and the more similar species are
192 in strategy, the more strongly they will compete. This property of competition also has
193 empirical support (Burns and Strauss 2011, Jiang et al. 2010, Johansson and Keddy 1991).
194 Larger values of ρ make the competition function more “box-like,” declining more slowly
195 at first, and then falling off quickly when the trait differences reach σ (Appendix S1: Fig.
196 S1). The model given by Eqs. 1 and 3 involves niche dynamics in that a suite of species
197 can coexist stably and robustly (i.e. even under small parameter changes) on the trait
198 axis only if they are far enough apart in trait values (as long as $\rho \geq 2$) (MacArthur
199 and Levins 1967, May 1973, Abrams 1983, Szabó and Meszéna 2006, Pigolotti et al.
200 2007, Hernández-García et al. 2009, Pigolotti et al. 2010, Gyllenberg and Meszéna 2005,
201 Meszéna et al. 2006, Barabás and Meszéna 2009, Barabás et al. 2012, 2013a). The $\rho < 2$
202 case is biologically unrealistic, as continuity in species interactions with regulating factors
203 would preclude it (Barabás et al. 2012, 2013a). This is because with $\rho < 2$, there is a
204 kink, or corner in the competition coefficient function where trait difference is zero. If one
205 considers competition as arising from resource use overlap, this kink can only arise when
206 there is an unrealistic discontinuity in species resource utilization (e.g. a bird species could
207 consume seeds of length 0.99999 cm, but not those of length 1 cm.) (Barabás et al. 2013a).
208 Therefore, to simulate niche communities we use $\rho \geq 2$. The parameter σ is related to
209 the width of species resource utilization ranges and determines the limiting trait difference
210 between coexisting competitors (MacArthur and Levins 1967). Appendix S1 includes
211 further discussion of the shape parameter ρ .

212 We use a stochastic implementation of the dynamics given by Eq. 1 with immigration

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

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

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

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

221 where m is the proportion of new individuals being added to the community that are
 222 immigrants, p_i is the relative abundance of species i in the regional pool, and J is the
 223 desired number of individuals in the local community. Note these expressions assume
 224 that the community is under viability selection, so deaths are density-dependent while
 225 recruitment is density-independent. The rate b_i reflects the rate of both local births (first
 226 term) and arrival of new individuals through immigration (second term) for a species
 227 present in the local community. The death rate d_i is the density-dependent portion
 228 of Eq. 1. We set these expressions up so that the total rate of new individuals being
 229 produced locally or entering the community through immigration ($\sum_i b_i + s$) is equal
 230 to βJ , and that the total immigration rate (the sum across species of the second term
 231 in b_i plus s) is equal to $m \beta J$, a fixed proportion of that total rate of new individuals
 232 entering the local community. These expressions also assume that the probability of an
 233 immigrating individual belonging to a given species is equal to its relative abundance in

234 the regional pool, p_i . We take the relative abundances in the source pool to follow the
235 Ewens sampling distribution with parameter θ (Etienne et al. 2007).

236 The continuous stochastic dynamics (Equations 5, 6, and 7) can be simulated using
237 the Gillespie algorithm (Gillespie 1977), in which one uses the relative rates of events to
238 decide which event occurs next (e.g. the probability that the next event is an increase in
239 abundance of species i is $b_i / (\sum_j (b_j + d_j) + s)$). The time that passes before the next
240 event can be calculated by drawing from a distribution determined by the total event rate
241 based on the current state of the community. In our Gillespie algorithm, when the event
242 is chosen to be immigration of a species not present in the local community (Eq. 7), the
243 species trait value u_i is chosen at random. Then its relative abundance is chosen using the
244 Ewens sampling formula and divided by the proportion of species in the regional pool that
245 are not currently in the local community ($1 - \sum_{j=1}^S p_j$). This procedure is valid because
246 the Ewens sampling formula applies to even a portion of an infinite neutral regional pool
247 (Etienne et al. 2007). Note all events occur at a rate proportional to β , so its value only
248 effects the amount of time between events (which we ignore, as we are focusing on the
249 equilibrium communities).

250 Simulations were initiated with 250 species at equal abundance with randomly
251 assigned trait values between 0 and 1, and were run for a large enough number of events
252 that visual analysis suggested the average SAD across runs was near equilibrium. We
253 plotted the average SAD across simulations at intermediate time points to determine
254 the appropriate number of events. We ran the niche simulations for 5×10^7 events and
255 the neutral simulations for 1×10^7 events. The SAD may continue to change subtly in
256 the niche case beyond this, but the change is towards greater difference from the neutral
257 SAD. To relate the SAD predictions of the model to familiar neutral SAD predictions,
258 we set J to the size of the tree community in the 50 ha CTFS-ForestGEO plot on Barro
259 Colorado Island (21,455 individuals > 10 cm dbh in 1995) (Hubbell et al. 2005), and the
260 immigration probability m and fundamental biodiversity number θ to values under which

261 neutral theory provides a good fit to the empirical species abundance distribution (0.098,
262 and 47.8 respectively; (Etienne 2005)). Note that the total community size in our model
263 is controlled by a combination of J and K . In the neutral case we can set both equal to
264 the desired community size, but in the niche case we tune K to achieve a target stationary
265 community of approximately 21,455 individuals.

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

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

275 **3 Results**

276 **3.1 Emergent Niche Structuring**

277 The neutral case ($\alpha(w_{ij}) = 1$) shows no distinct pattern of abundances along the trait
278 axis (Figure 1a). Under niche dynamics however, the model produces clumps of densely
279 packed and abundant species, separated by regions with fewer and less abundant species
280 as shown by the example with $\rho = 4$ and $\sigma = 0.15$ in Figure 1b. As stated in the
281 Introduction, this model produces a clumping pattern that was mentioned briefly by
282 Barabás et al. (2013a). The pattern is similar to that pointed out by Scheffer and van
283 Nes (2006) but is maintained by immigration rather than the addition of intraspecific
284 negative density dependence. The number of clumps is equal to the number of stably
285 coexisting species that would be expected at equilibrium in the deterministic version of

286 our model (Eq. 1), which numerical exploration shows is determined primarily by σ . We
287 call the clumping pattern in our model “emergent niches” to emphasize that groups form
288 as a result of the dynamics rather than being prescribed ahead of time, and that those
289 groups are organized around equally-spaced positions on the trait axis that would allow
290 for stable coexistence in the deterministic model. At the end of each simulation, we can
291 interpret the emerged clumps as occupying their own niches, or equally-sized regions of the
292 trait axis. We describe how we designate niche regions in Section 3.3 where we consider
293 “within-niche” and “between-niche” interactions. The number of clumps and hence niches
294 that emerge can be tuned by choosing σ appropriately. Due to the circular niche axis and
295 the fact that species interactions depend only on distance and not the absolute positions
296 along the niche axis, only the relative positions of the clumps are determined by σ , with
297 the exact locations varying through time and across simulations.

298 Varying ρ produces a range of competition functions that decline with increasing
299 trait differences (Appendix S1: Fig. S1). There is no discernable niche structure with
300 Gaussian ($\rho = 2$) competition coefficients (Appendix S1: Fig. S2). This is likely because of
301 tight packing behavior (i.e. stable coexistence of a set of species arbitrarily close to each
302 other on the trait axis) that can be generated by the deterministic model in that case.
303 Tight packing behavior is sensitive to parameter values (i.e. it is not robust, breaking
304 down to limiting similarity with small variation in carrying capacity on the trait axis)
305 (Roughgarden 1979, Gyllenberg and Meszéna 2005, Meszéna et al. 2006, Barabás et al.
306 2012). To avoid these special behaviors, we focus on the $\rho = 4$ case, as it is a conservative
307 choice that yields representative niche structuring from this model (Figure 1b, Appendix
308 S1: Fig. S3). For more information regarding model assumptions and behavior related to
309 variation in ρ , see Appendix S1.

3.2 Species abundance distributions

When niches are few relative to the number of species, the extreme niche model of Chisholm and Pacala (2010) (the C&P 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 (Figure 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 C&P model. In particular, with even just five niches, differences between the niche and neutral SADs averaged over 1,000 simulations are apparent (Figure 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 (6th-8th abundance classes on the Preston-style SAD plot shown) than the neutral case, and lower proportions of intermediately rare and intermediately high abundance species (3rd-5th and 9th-10th 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 C&P model prediction for the 5-niche case is virtually indistinguishable from the neutral case (Figure 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 (Figure 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 C&P model (Figure 2b,c). The predictions

337 from our model and the C&P model are very close in the large abundance classes, with
338 the directions of differences from neutrality in those classes being the same in both
339 models. However, our resulting average SAD also differs strongly from the neutral case
340 along the rest of the curve while the C&P prediction does not (Figure 2, Appendix
341 S1: Fig. S5). In particular, it still generates a higher proportion of species of medium
342 abundance (6th-8th abundance classes) and lower proportion of intermediately rare species
343 (3rd-5th abundance classes) than seen in the neutral case.

344 **3.3 Further exploration: The importance of heterogeneity in** 345 **interactions across niches**

346 The strength of interactions in our model with niche dynamics is determined by the
347 distance in trait value between species regardless of the niche in which they fall, resulting
348 in some key differences from the C&P model. First, in our model, species in different
349 niches, or clumps, compete with one another (i.e. there are “between-niche” interactions),
350 whereas Chisholm and Pacala include only interactions within niches. Second, our model
351 includes heterogeneity in a) the strength of competition between species in different niches
352 (“between-niche” interactions), and in b) the strength of competition between species in
353 the same niche (“within-niche” interactions), in contrast to the neutrality imposed within
354 niches by Chisholm and Pacala. Both of these types of interaction heterogeneity have
355 the same underlying source in our model, namely the dependence of competition on trait
356 differences, but after niche structure emerges, within and between-niche interactions can
357 be delineated.

358 To illustrate the influence of each of these differences between our model and the C&P
359 model, we simulated a variety of scenarios in which the interaction structure is effectively
360 simplified in different ways. Due to the extensive computational resources required to run
361 this large number of simulations, we focused only on the 5-niche case for this analysis.
362 First, to consider a case of our model with dynamics as similar as possible to the model

363 of Chisholm and Pacala, we used niche dynamics (Eq. 3) and we restricted the possible
364 trait values to the discrete set $\{0.1, 0.3, 0.5, 0.7, 0.9\}$. By doing this, each species falls into
365 one of five niches in such a way that all species interact neutrally within a niche, as in the
366 C&P model (i.e. for i, j in the same niche, $\alpha(w_{ij}) = \alpha(0) = 1$). We also set $\rho = 100$.
367 This makes our competition coefficients go sharply to 0 for species that differ by more
368 than $\sigma = 0.15$ (see Appendix S1: Fig. S1, and note that even larger values of ρ result in
369 a similar shape for the competition coefficients), and hence eliminates competition between
370 species in different niches, as the C&P model does. This case of our model and the C&P
371 model are essentially the same, with the small differences being that our model includes
372 community-level density-dependence while the C&P model uses zero-sum dynamics, and
373 that the C&P model incorporates niche structure in the metacommunity while our model
374 does not. We also do not constrain total niche abundances to be equal as is done in the
375 C&P model.

376 Second, we considered a case of our model that has neutral interactions within niches,
377 but allows for interactions (with no heterogeneity) between niches. In implementation, this
378 scenario differs from the previously described case only in that it uses $\rho = 4$ instead of
379 $\rho = 100$, so that the competition strength falls less steeply with increasing trait difference.

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

389 Finally, we simulated two additional cases of our model to explore the specific roles

390 of heterogeneity in “between-niche” interactions, and heterogeneity in “within-niche”
391 interactions. Both of these cases were initiated from the final communities of the full
392 5-niche simulations so that niches were already present and we could distinguish between
393 within- and between-niche interactions. In the case with only between-niche interaction
394 heterogeneity, interactions between species in different niches depend on trait difference,
395 and interactions within niches are neutral ($\alpha(w_{ij})$ is given by Equation 3 if species i and
396 j are in separate niches and is constant otherwise), and vice-versa in the “within-niche”
397 heterogeneity case. We delineated species niches according to the abundance structure
398 in the final 5-niche configurations, where abundances tend to be highest at the centers
399 of the niches. For each simulation, we identified the first niche by designating the trait
400 of the most abundant species to be at the center of that niche. We then designated the
401 remaining niche centers to be equally spaced across the niche axis with the first. Each
402 niche occupies a region of width 0.2. For each case, we ran 1,000 simulations each for
403 5×10^5 events.

404 Analyzing the output of these simulations leads to a number of insights. Figure
405 3a shows the SADs for the neutral model, the C&P model prediction, and the two
406 simplest cases of our model we considered, namely the case analogous to the C&P
407 model, and the case with homogenous between-niche interactions added to our analogue
408 of the C&P model. We see that these simple cases of our model produce SADs very
409 similar to one another, and to the C&P model prediction, though with a slightly
410 greater deviation from the neutral SAD (Figure 3a). This suggests that the presence of
411 homogeneous between-niche interactions do not play much of a role in shaping the SAD
412 of our full model, and neither do the differences in the assumptions behind the C&P
413 model prediction and our analogous version of the C&P model (i.e. our model includes
414 community-level density-dependence while the C&P model uses zero-sum dynamics, and
415 the C&P model incorporates niche structure in the metacommunity and constrains niche
416 abundances to be equal while our model does neither).

417 Figure 3b shows the SADs for our cases of intermediate levels of interaction
418 heterogeneity, along with the neutral and full niche dynamics cases. (Note that a trait
419 span of 0 corresponds to our analogue of the C&P model with homogenous between-niche
420 interactions added.) Increasing interaction heterogeneity (by increasing the width of the
421 niche regions) brings the SAD closer to the SAD of our full model. Furthermore, Figure
422 3b shows that the SAD from the model with half-sized niche regions is very similar to the
423 SAD of our full model.

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

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

441 In Figure 4b we see further evidence for the influence of between-niche interaction
442 heterogeneity and the counteracting influence of within-niche interaction heterogeneity.
443 The SAD for the case with between-niche interaction heterogeneity essentially differs from

444 the neutral model SAD in similar ways to our full model, but to a larger degree, with
445 the exception of the largest abundance class. For greater readability, we do not plot the
446 within-niche heterogeneity case SAD in Figure 4b. As stated above and shown in Figure
447 4a, it produces the wrong trend of abundance with trait values within niches, and in this
448 sense, is a poor approximation to our full model.

449 **4 Discussion**

450 To determine whether observed SADs can be used to infer community assembly processes,
451 we first need to know how they change with the presence of niche dynamics. Purves
452 et al. (2005) and Chisholm and Pacala (2010) recently argued that niche and neutral
453 SADs are very similar when there are many species per niche, and in fact identical in
454 the infinite diversity limit. They demonstrated this analytically for the case of discrete,
455 non-interacting niches with neutral dynamics within each niche. Here we have shown
456 that SADs show distinct differences between niche and neutral communities when niche
457 structuring emerges from the dynamics of a model with trait-dependent competition
458 instead of being modeled in a simplified rigid manner. In particular, visually apparent
459 differences arise in the SAD even with a small number of niches relative to the number
460 of species. Furthermore, we have shown that the heterogeneity in interaction strength
461 produced by trait-dependent competition strongly influences the shape of the SAD, and
462 we illustrated how heterogeneity in between-niche and within-niche interactions each
463 contribute to that influence.

464 It is clear from our study that the presence of niches in an community of competing
465 species can influence the shape of the SAD, and that while the extreme niche structuring
466 of the C&P model makes it feasible to derive valuable analytical results, it is too extreme
467 to reflect processes that may give rise to differences from a neutral SAD. This perhaps
468 should not be surprising given that the rigid niche structure of the C&P model could more

469 readily be interpreted as a set of disparate groups of organisms such as phytoplankton put
470 together with a group of trees in a rainforest and a collection of island birds, etc., than
471 niches in a community of interacting species. Indeed, Haegeman et al. (2011) point out
472 that a model of independent, unregulated species gives the same SAD predictions as a
473 zero-sum neutral model for all levels of diversity, and hence that it is not surprising that
474 extreme niche structuring leads to the same distributions as a neutral model in the high
475 diversity limit. When there are more species than niches, species in separate niches would
476 likely instead retain some level of interaction, with heterogeneity in the intensity of those
477 interactions due to variation in similarity of resource use or other competitive factors with
478 the dominant species in a nearby niche. In our model, where niche structure emerges from
479 competition that depends on species trait differences, species organize into niches in such
480 a way that there are significant interactions across niches, and the heterogeneity in those
481 interactions shapes species' relative abundances.

482 We highlighted that heterogeneous interactions across niches are dominant in shaping
483 the pattern of species abundances along the trait axis. To demonstrate this, we used
484 5-niche communities, though further investigation would be needed to generalize these
485 results. While understanding exactly how heterogeneous interactions within or between
486 niches affect differences in particular abundance classes is not intuitive, we showed how
487 within and between-niche interactions each contribute to shaping abundances on the trait
488 axis by looking at the communities that arise in each case separately. The heterogeneous
489 interactions within the niche appear to buffer the advantage that species at the centers
490 of niches would otherwise have based only on between-niche interactions, and their
491 inclusion results in an SAD that is generally less exaggerated than that of communities
492 with between-niche heterogeneity alone. In particular, communities with between-niche
493 heterogeneity alone have a sharper central peak in their SAD than our full model.
494 Appendix S2 includes further discussion of the influence of interaction heterogeneity on
495 particular SAD bins.

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

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

516 A specific type of additional complexity that may be important in many systems is
517 the presence of hierarchical interactions (e.g. Harpole and Tilman (2006) and Kunstler
518 et al. (2012)), which could introduce a dependence of competition strength on the trait
519 itself and not just trait differences. Chave et al. (2002) studied the influence of such
520 niche dynamics on the SAD. Although their study focused on the range of SAD patterns
521 predicted as dispersal parameters varied, they also mentioned differences found for fixed
522 parameter values (and significant niche structure) that involved an increase in the number

523 of species of moderate abundance like that observed here. Their hierarchical competition
524 model, however, involved unrealistic discontinuities (Barabás et al. 2013a, D’Andrea et al.
525 2013). Another aspect of complexity in competitive interactions worthy of consideration
526 is the potential for the decrease in competition with increasing trait differences to be
527 non-monotonic, which can occur when competition is through consumption of populations
528 that can be driven extinct (Abrams et al. 2008). Further study is needed to more fully
529 understand how underlying dynamics affect the shape of a community’s SAD.

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

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708 **List of Figures**

709 1 Emergent niche structuring. Example neutral (a) and 5-niche (b)
710 configurations at the ends of the simulations, showing the abundances of
711 all species in the community organized by trait value. (a) No pattern is
712 visible along the trait axis in the neutral case. $K = 21,455$; run length:
713 1×10^7 events; total abundance for this example: 21,235. (b) Clumping of
714 abundant species is visible along the trait axis. $K = 5410$, $\sigma = 0.15$, $\rho = 4$;
715 run length: 5×10^7 events; total abundance for this example: 21,346. 33

716 2 Species abundance distributions (SADs) resulting from the neutral model,
717 our niche model, and Chisholm and Pacalas (C&Ps) niche model. In all
718 SAD figures in this paper, SADs are shown in a Preston-style plot of
719 the proportion of species in up to 12 logarithmically-scaled abundance
720 classes Volkov et al. (2003). Our niche and neutral SADs are averaged
721 over 1,000 simulations each, and the C&P SAD is produced using the
722 analytical formula in Chisholm and Pacala (2010). All neutral simulations
723 use $K = 21,455$. All niche simulations use $\rho = 4$. (a) 5-niche communities
724 ($K = 5410$, $\sigma = 0.15$), (b) 20-niche communities ($K = 1310$, $\sigma = 0.037$)
725 and (c) 50-niche communities ($K = 519$, $\sigma = 0.015$). Mean species richness
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728 3 Effects of homogeneous between-niche interactions and interaction
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732 homogeneous between-niche competition added (“Between-niche comp.
733 added,” $\rho = 4$, $K = 4300$). (b) SADs for the neutral case, our regular niche
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735 cases with intermediate levels of interaction heterogeneity, “1/4 trait span”
736 and “1/2 trait span.” In the latter two cases, species trait values are chosen
737 from equally spaced regions on the trait axis sized as 1/4 or 1/2 of a niche
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740 4 Effects of between-niche and within-niche interaction heterogeneity on
741 SADs in the 5-niche case. (a) Binned abundances in a single niche with
742 bins averaged over 1,000 simulations. “Het. between” has heterogeneity in
743 between-niche interactions only; “Het. within” has interaction heterogeneity
744 within niches only ($\alpha = 1$ for between-niche interactions), and “Full het.” is
745 our full model. (b) SADs averaged over 1,000 simulations. (Online version
746 in color.) 36

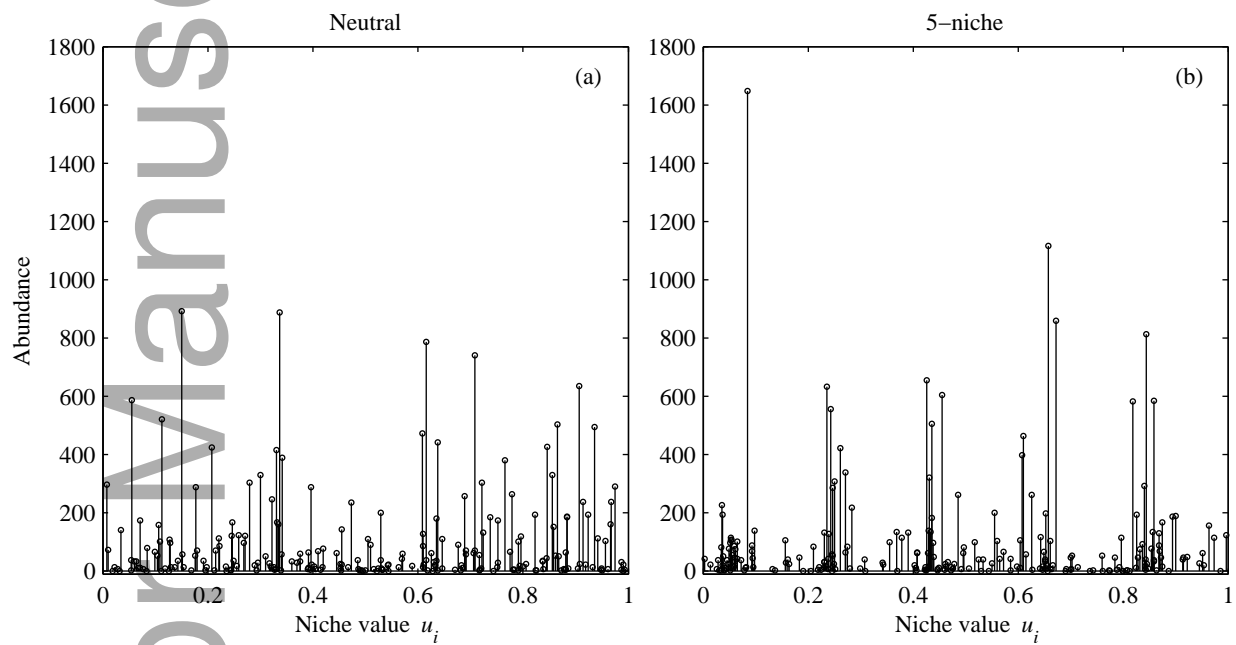


Figure 1

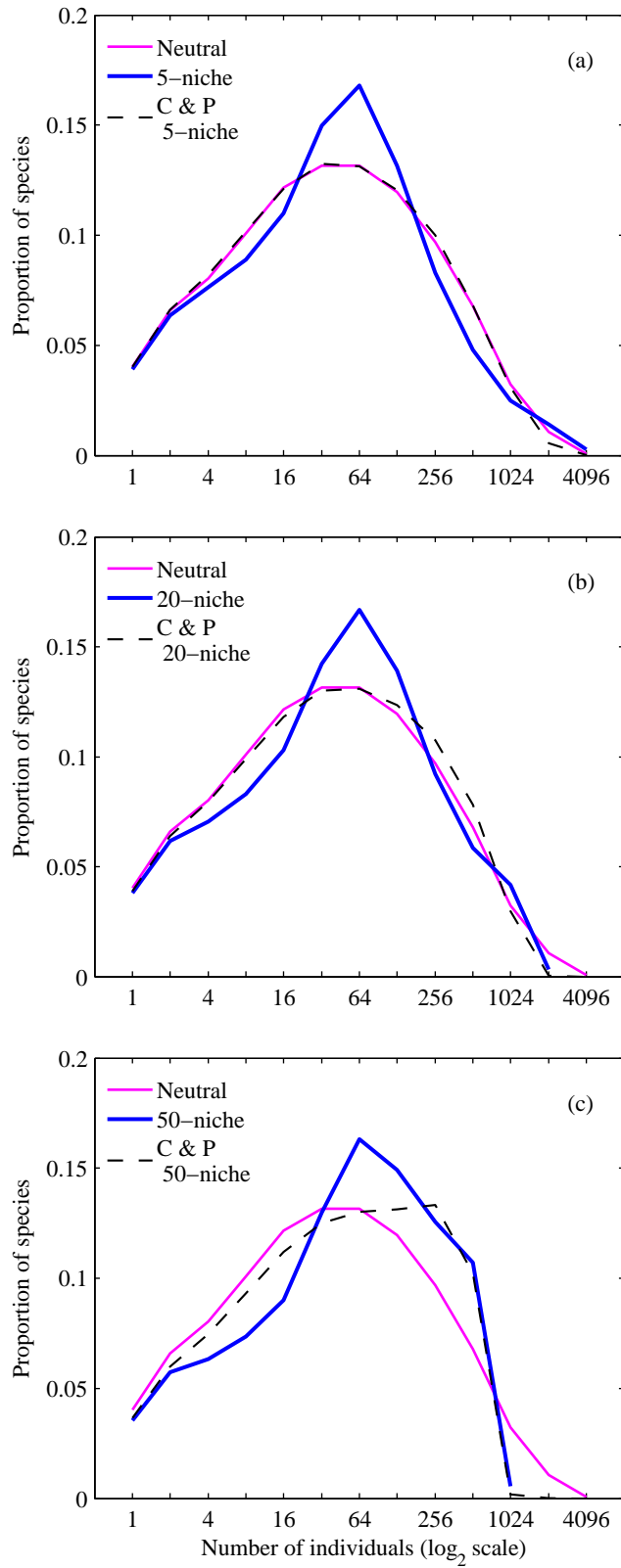


Figure 2

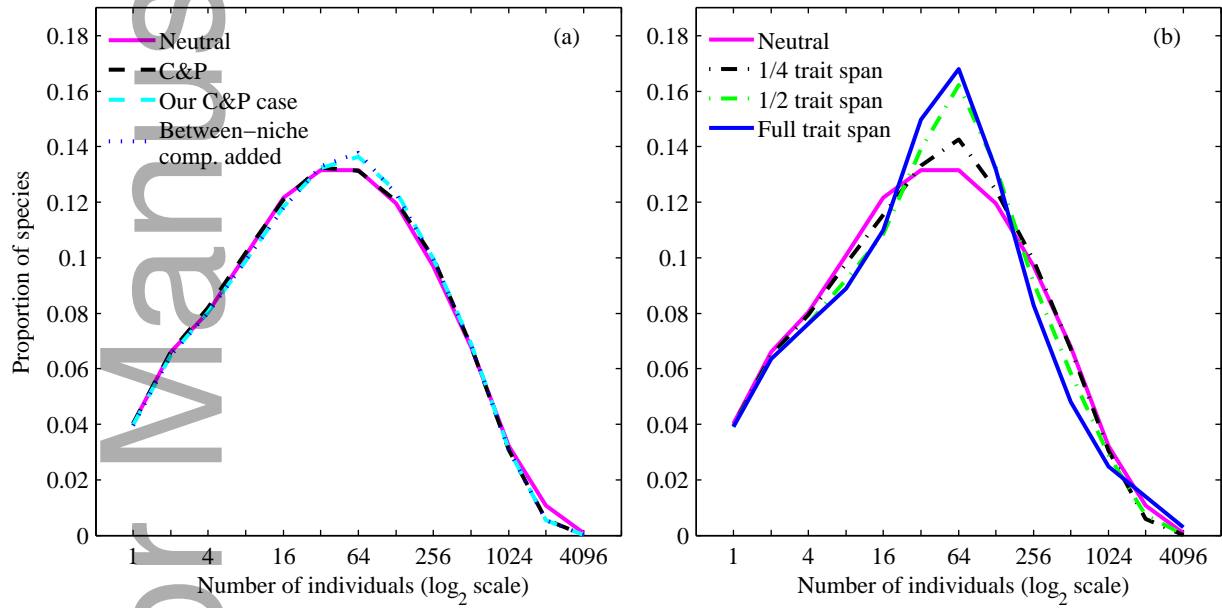


Figure 3

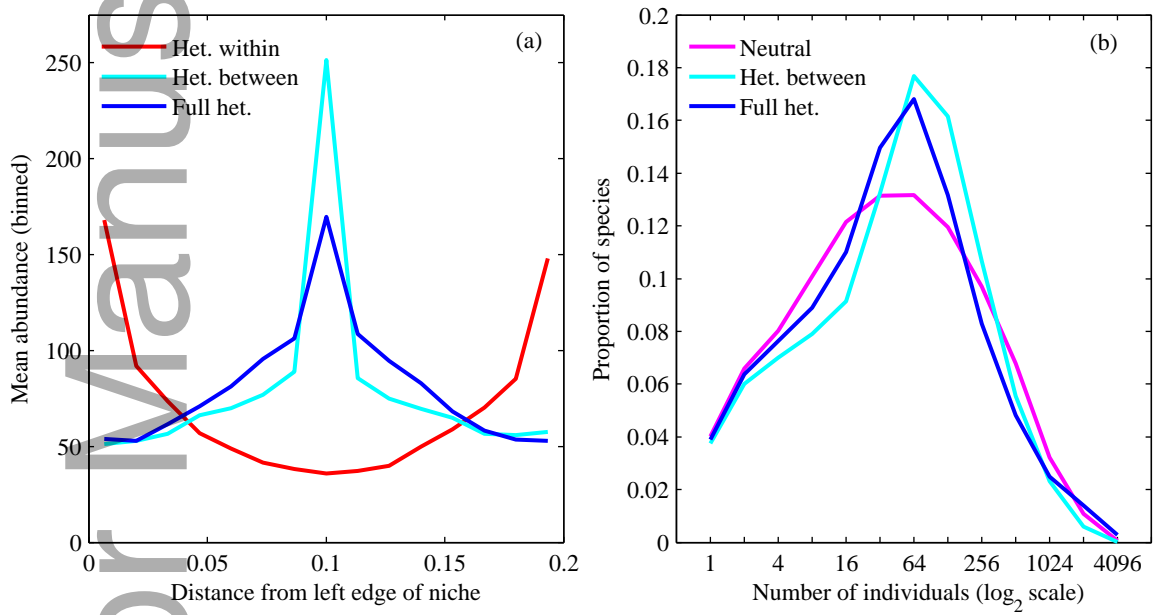
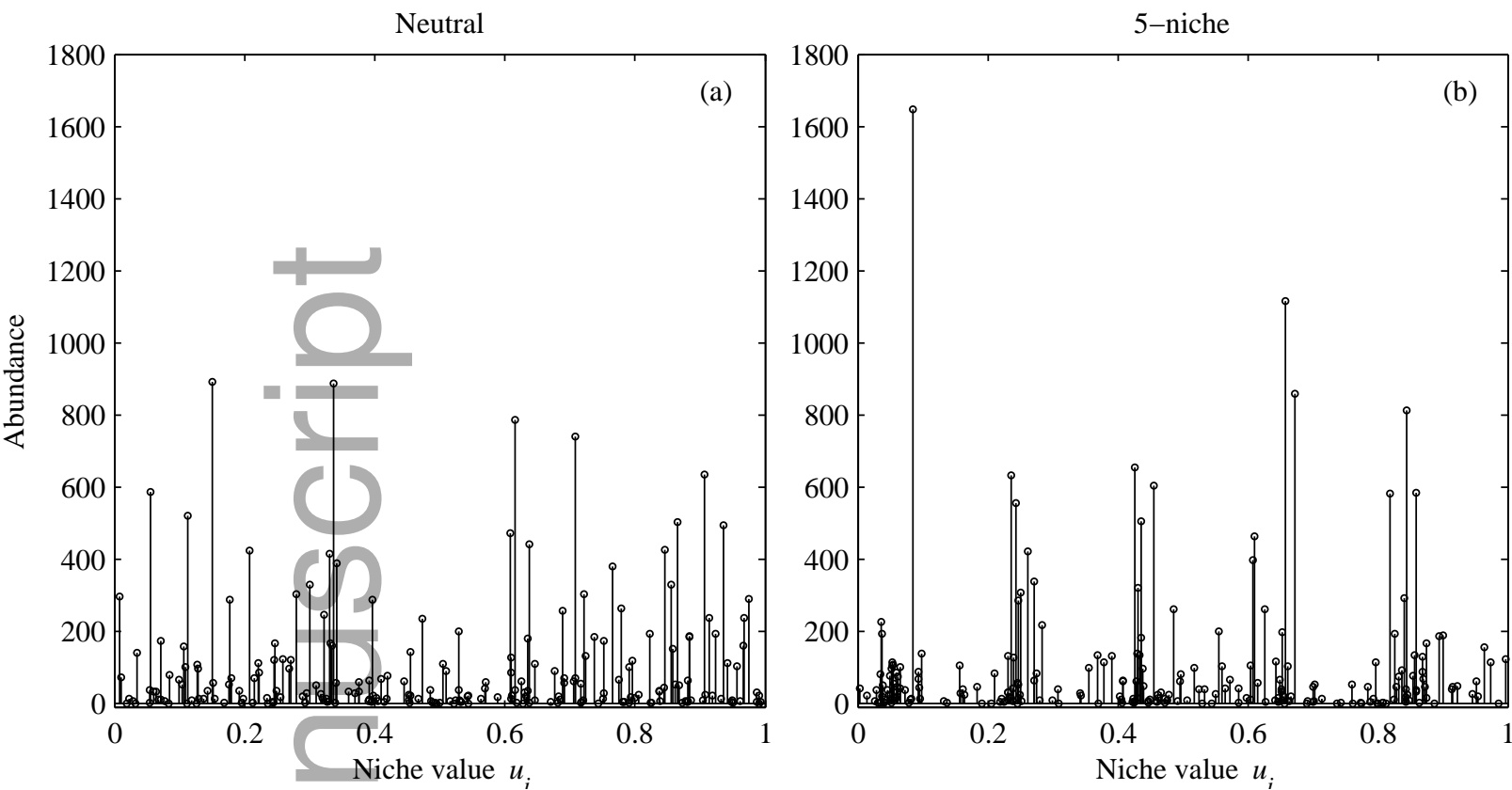
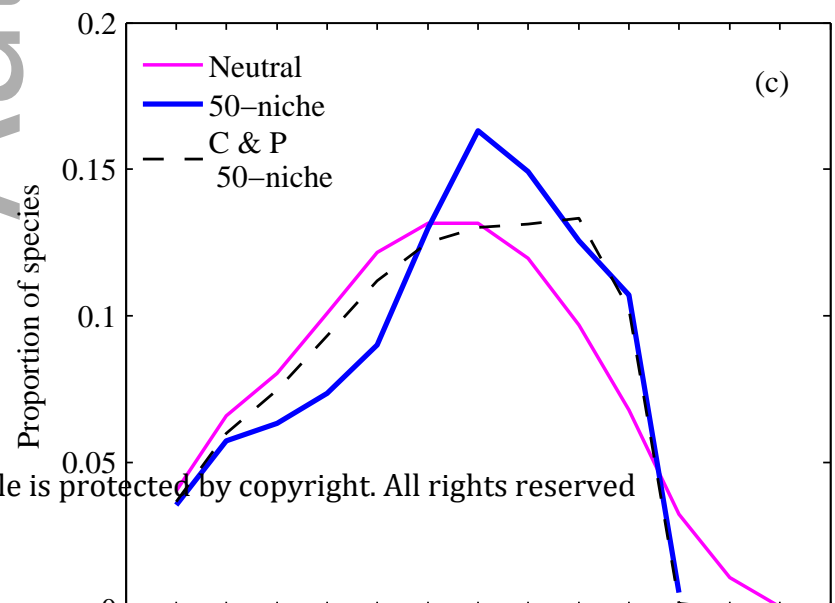
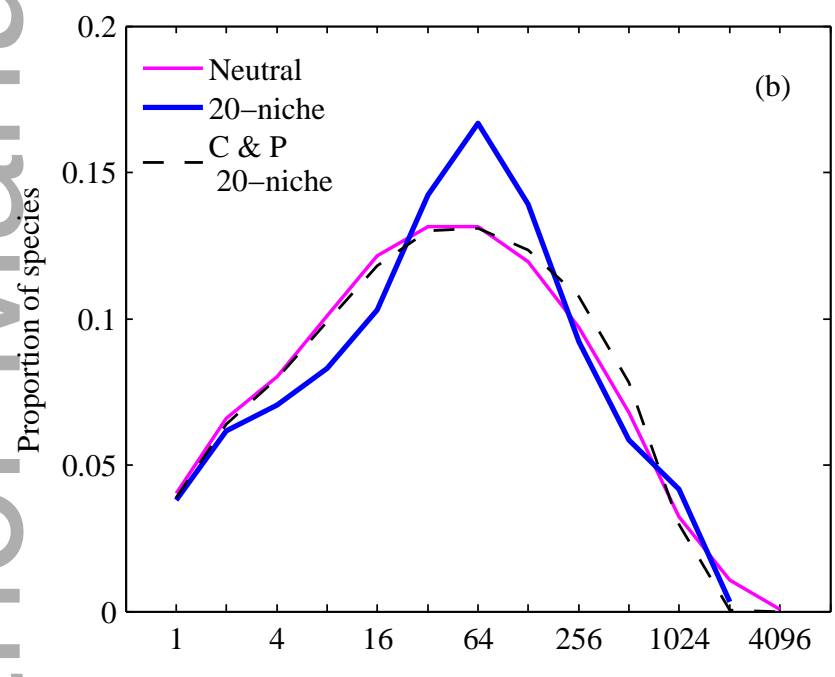
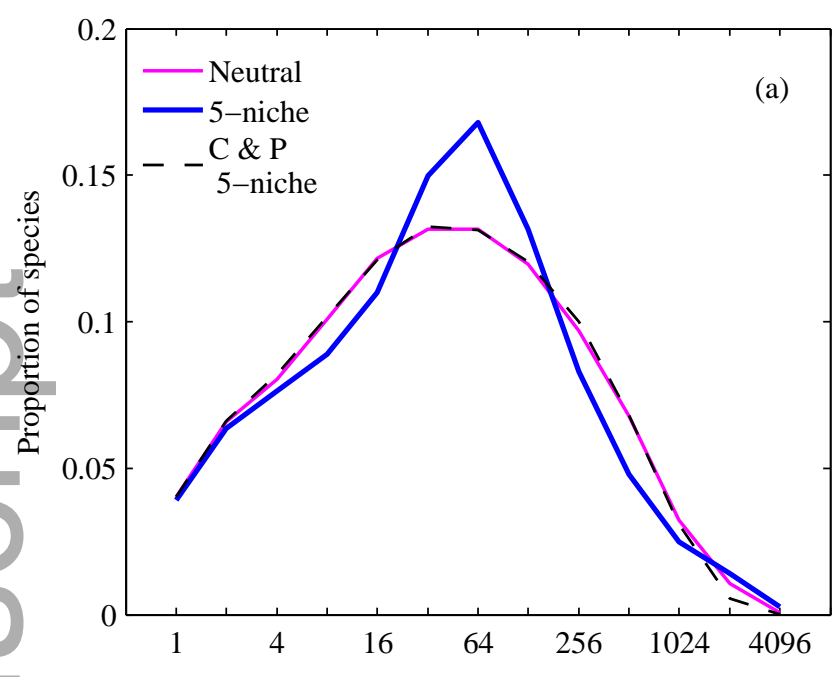
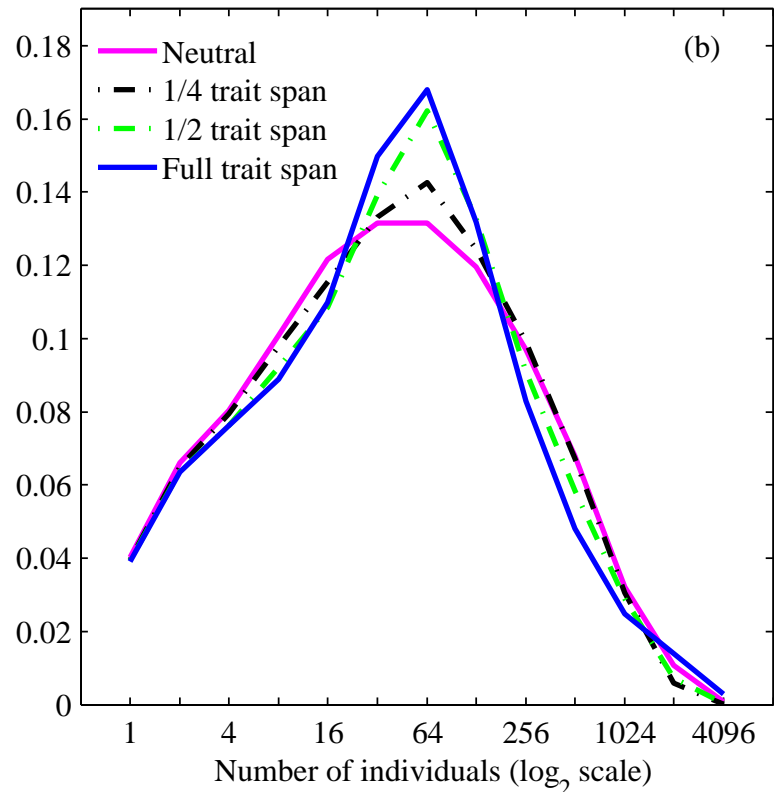
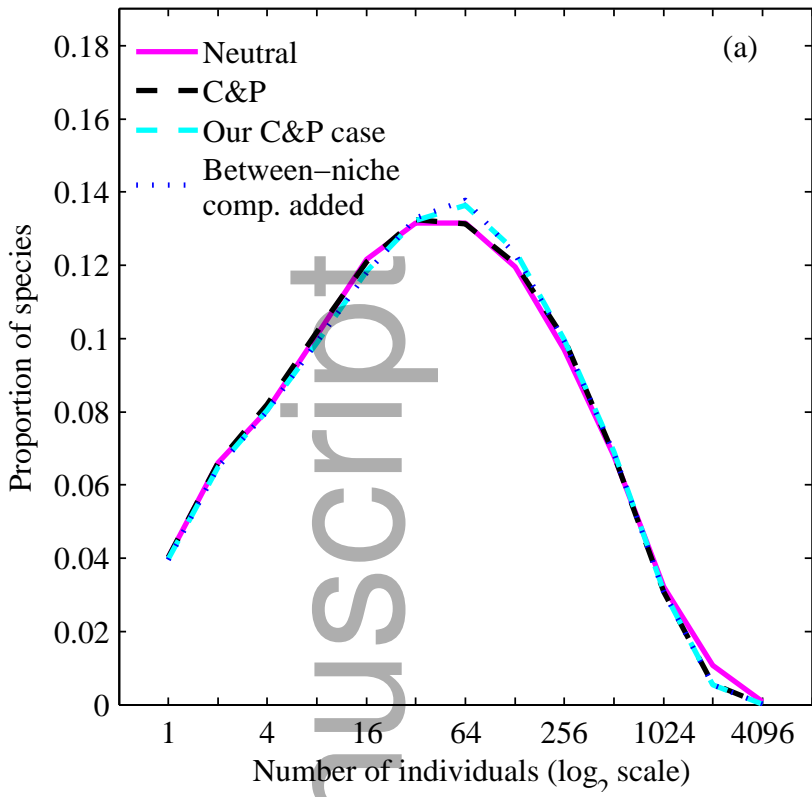


Figure 4

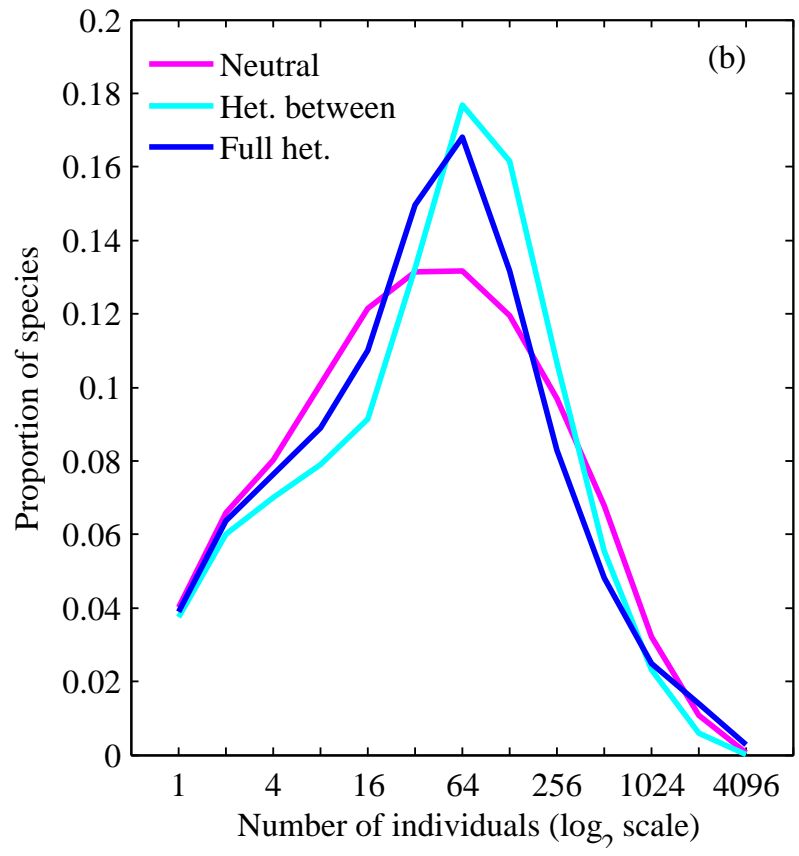
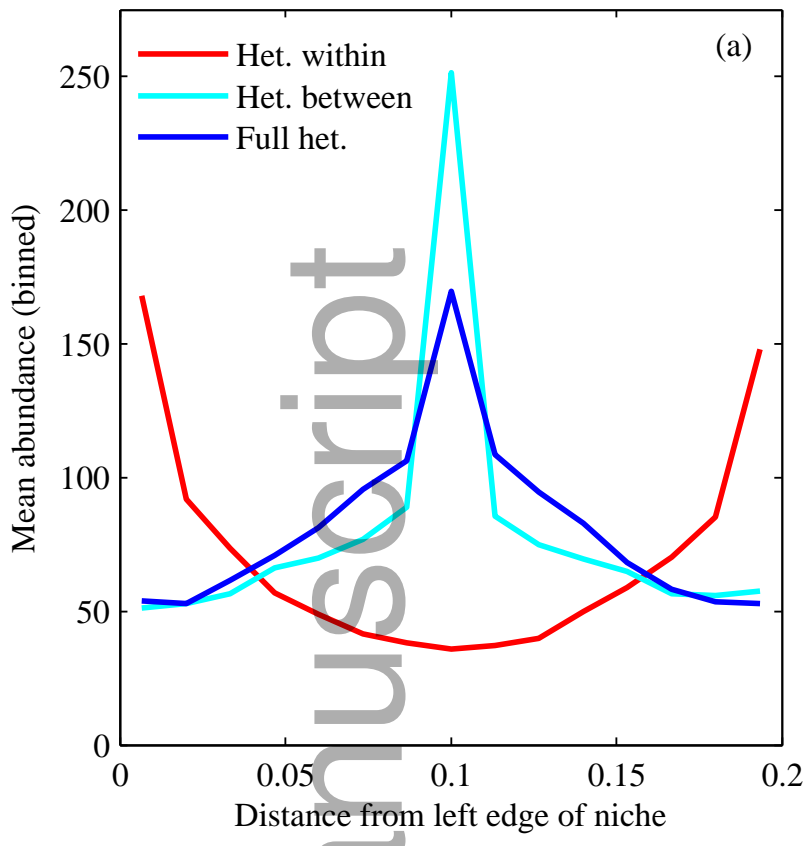


ecy_2238_f1.eps





ecy_2238_f3.eps



ecy_2238_f4.eps

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