## Appendix S1

for

"Emergent niche structuring leads to increased differences from neutrality in species

abundance distributions"

Rosalyn C. Rael, Rafael D'Andrea, György Barabás, Annette Ostling

## S1 Model assumptions and behavior for different values of the competition coefficient shape parameter $\rho$

In the main text we focused on the value  $\rho = 4$  in the competition coefficient function when looking at species abundance distribution patterns. This parameter controls how "box-like" the competition coefficient function is: larger values of  $\rho$  correspond to more box-like shapes, as  $\rho \to \infty$  (Figure S1). Here we comment on biological assumptions and model behavior related to different values of  $\rho$ .

In the deterministic Lotka–Volterra model (Eq. 1 in main text), though values of  $\rho$  less than two are mathematically meaningful, they have been shown to be biologically unrealistic (Adler and Mosquera, 2000; Barabás et al., 2012, 2013), as they are derived in situations in which species to utilize their resources or environments in discontinuous ways (i.e. with consumption varying discontinuously as a function of which resource among a continuous array of resources (e.g. seeds of different sizes) one is considering), or more broadly, situations in which species interact with regulating factors discontinuously. Therefore, only the  $\rho \geq 2$ case is of interest.

The particular choice of  $\rho = 2$  has historical significance, as it was used by MacArthur and Levins (1967) in deriving the principle of limiting similarity. It also derives from the assumption that species have Gaussian-shaped resource utilization curves under fast resource dynamics, where the competition coefficient boils down to a measure of the overlap in utilization curves (MacArthur and Levins, 1967). Although this serves as a biologically plausible-sounding example case, we really know very little about the correspondence between competition coefficients and ecological interactions nature, other than that there seems to be a relationship with trait differences (Johansson and Keddy, 1991; Jiang et al., 2010; Burns and Strauss, 2011). This makes intuitive sense because if traits drive ecological strategies, then species with similar traits will have similar strategies and hence compete more strongly. Species interactions with their resources (or more broadly "limiting factors" (Levin, 1970)), and the competitive interactions that occur through these resources, are likely not typically as simple as modeled by MacArthur. Any number of assumptions about the nature of competition can produce different forms of the competition coefficient (Abrams, 1975; Hernández-García et al., 2009). Here we do not have any specific biological picture in mind for what leads to different values of  $\rho$ . Variation in  $\rho$  provides a range of competition functions that decline with increasing trait differences.

An issue with the parameter choice of  $\rho = 2$  is that it does not always lead to the emergence of niche structuring. For example, an infinite number of species arbitrarily close in traits can coexist with  $\rho = 2$ , a constant carrying capacity, and fully periodic boundary conditions (i.e. where competition is an infinite sum of the coefficients as functions of the distances between two species as you continue to go around the circular axis) (Hernández-García et al., 2009; Pigolotti et al., 2010). However, if the boundary conditions are truncated, meaning that competition is just a single term that is a function of the *closest* distance between two species ( $w_{ij} = \min(|u_i - u_j|, 1 - |u_i - u_j|)$ ), then the clumpy niche pattern emerges on the niche axis (Pigolotti et al., 2010), and transient species can persist for thousands of generations (Fort et al., 2009; Scheffer and van Nes, 2006). Limiting similarity also arises if the trait axis is taken to be finite and noncircular (Szabó and Meszéna, 2006).

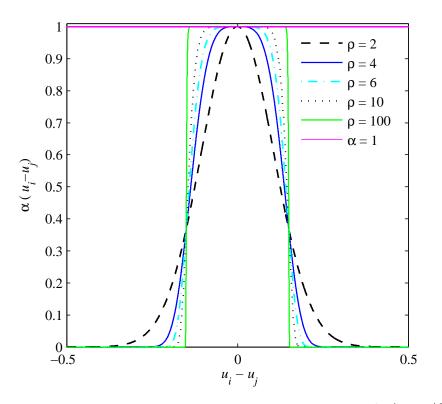
Note that we use the truncated form of the boundary conditions here. However, for  $\rho = 2$  we actually do not see a clear clumping pattern emerge over the course of our stochastic simulations as shown in Figure S2, possibly because we have immigration of new species in our model that may outpace the formation of the niche structure, though this needs further investigation. Even though no visible niche structuring forms with  $\rho = 2$  in our model, we do see a slight difference from neutrality in the SAD (Figure S4) for this case.

If a Gaussian function of a species trait is used instead of a constant for carrying capacity, the Lotka-Volterra model taken with competition coefficients using  $\rho = 2$  can produce a community with no limits to similarity in coexisting species (i.e. no niche structure) (Roughgarden, 1979). However, even the slightest change to the function, such as from a single species having a slightly higher than expected carrying capacity, leads to a nichestructured community (Gyllenberg and Meszéna, 2005; Meszéna et al., 2006; Barabás and Meszéna, 2009). Though  $\rho = 2$  is very commonly used, patterns of coexistence for the model with this parameter are highly sensitive to the slightest changes in the carrying capacity and implementation of boundary conditions. Given that estimated parameters in real systems will naturally vary, this lack of robustness is a concern and suggests that model behavior with  $\rho = 2$  may not be representative of model behavior across a broad range of feasible  $\rho$ values. For all  $\rho$  values greater than two, niche structuring occurs regardless of choices of boundary conditions and carrying capacity functions. We chose to focus on results for  $\rho = 4$  because the niche structuring found in this case is more typical of what the model produces across  $\rho$  values. Figure S3 shows some of the abundance patterns for other  $\rho$  values we explored, and Figure S4 shows some of the corresponding SADs for those cases. The niche structure resulting from our model becomes stronger as  $\rho$  increases. Though the visible differences are somewhat subtle, the densities near the centers of the niches increase as  $\rho$  increases. For  $\rho = 100$ , the species near the centers of the niches can reach higher abundances than are observed in the other cases. Note it seems our choice of  $\rho = 4$  is conservative compared to higher  $\rho$  values in that resulting SADs are increasingly different from the neutral case as  $\rho$ is increased, at least in all but the two highest abundance classes, where trends with  $\rho$  are more complicated.

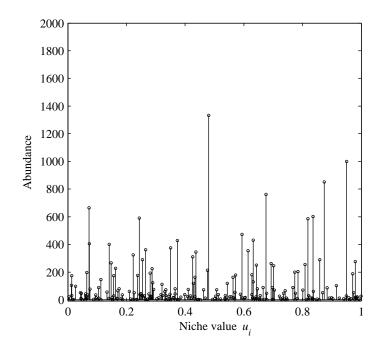
## Literature Cited

- Abrams, P., 1975. Limiting similarity and the form of the competition coefficient. *Theoretical Population Biology* 8:356–375.
- Adler, F. R. and J. Mosquera, 2000. Is space necessary? Interference competition and limits to biodiversity. *Ecology* 81:3226–3232.
- Barabás, G., R. D'Andrea, and A. M. Ostling, 2013. Species packing in nonsmooth competition models. *Theoretical Ecology* 6:1–19.
- 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.
- 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* **108**:5302–5307.
- Fort, H., M. Scheffer, and E. H. van Nes, 2009. The paradox of the clumps mathematically explained. *Theoretical Ecology* 2:171–176.
- Gyllenberg, M. and G. Meszéna, 2005. On the impossibility of coexistence of infinitely many strategies. *Journal of Mathematical Biology* **50**:133–160.

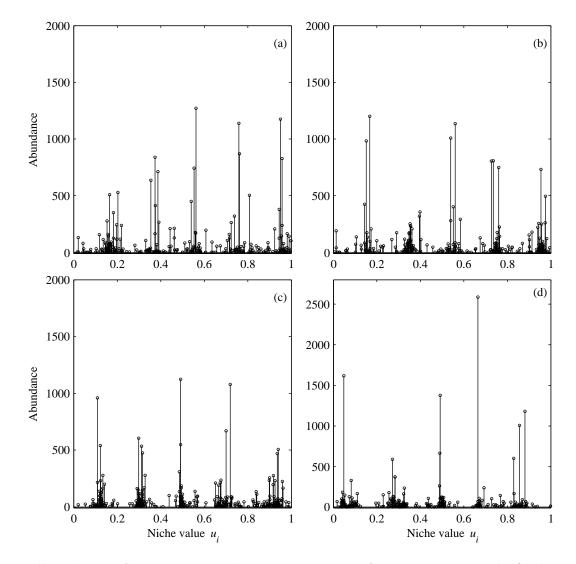
- Hernández-García, E., C. López, S. Pigolotti, and K. H. Andersen, 2009. Species competition: coexistence, exclusion and clustering. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 367:3183–3195.
- Jiang, L., J. Tan, and Z. Pu, 2010. An experimental test of darwins naturalization hypothesis. The 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* pages 27–34.
- Levin, S. A., 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* pages 413–423.
- MacArthur, R. and R. Levins, 1967. The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist* pages 377–385.
- Meszéna, G., M. Gyllenberg, L. Pásztor, and J. A. Metz, 2006. Competitive exclusion and limiting similarity: a unified theory. *Theoretical Population Biology* **69**:68–87.
- 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.
- Roughgarden, J., 1979. Theory of population genetics and evolutionary ecology. Macmillan New York.
- 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* **103**:6230–6235.
- Szabó, P. and G. Meszéna, 2006. Limiting similarity revisited. Oikos 112:612–619.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan, 2003. Neutral theory and relative species abundance in ecology. *Nature* **424**:1035–1037.



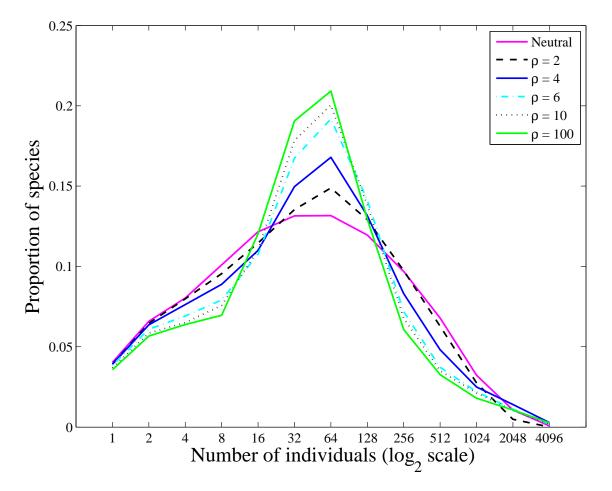
Appendix Figure S1: Competition coefficients  $\alpha(u_i - u_j) = \exp\left(-\left|\frac{u_i - u_j}{\sigma_{\alpha}}\right|^{\rho}\right)$  with  $\sigma_{\alpha} = 0.15$  and various values of the shape parameter  $\rho$ ; and  $\alpha(u_i - u_j) = 1$ .



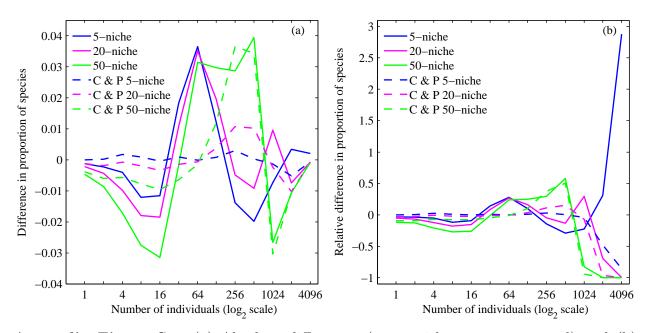
Appendix Figure S2: No clustering is visible when  $\rho = 2$ . Example final configuration of a 5-niche communities using the competition coefficients shown in Figure S1, with shape parameter  $\rho = 2$ , showing the abundances of all species in the community (conveyed by the height of the stems), organized by trait value. K = 2500.



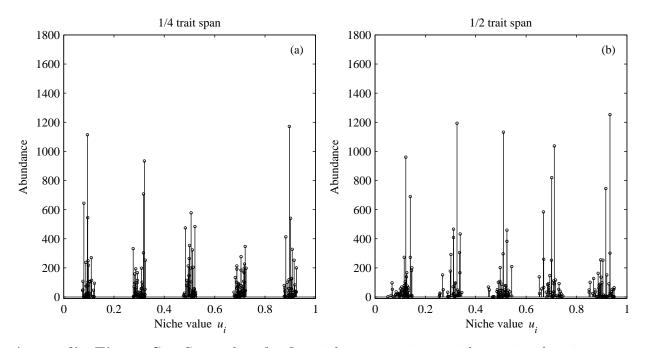
Appendix Figure S3: Emergent clustering is strong for  $\rho \ge 4$ . Example final configurations of 5-niche communities using the competition coefficients shown in Figure S1, with shape parameters (a)  $\rho = 4$ , (b)  $\rho = 6$ , (c)  $\rho = 10$ , and (d)  $\rho = 100$ , each showing the abundances of all species in the community (conveyed by the height of the stems), organized by trait value.



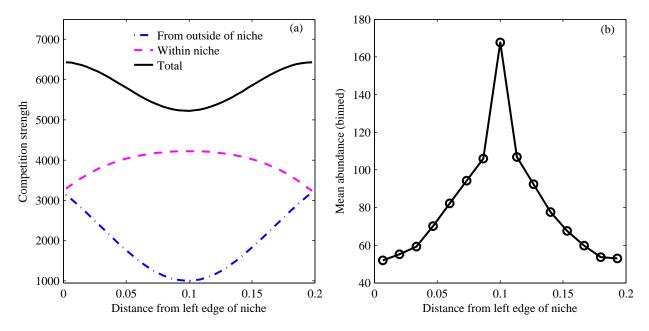
Appendix Figure S4: Variation in the species abundance distribution (SAD) with competition coefficient shape parameter  $\rho$ . Shown are SADs for the neutral case and for 5-niche communities with shape parameters  $\rho = 2, 4, 6, 10$ , and 100. (K = 21, 455 for the neutral case, and K = 6000, 5410, 5000, 4783, 4500 respectively for the niche cases.) As in main text, SADs are shown in a Preston-style plot of the proportion of species in logarithmically-scaled abundance classes delineated as in Volkov et al. (2003), lines are used to connect values in each abundance class, and values are the average over the ending configuration of 1000 simulations.



Appendix Figure S5: (a) Absolute differences (mean niche – mean neutral) and (b) relative differences ((mean niche – mean neutral)/mean neutral) between the mean niche and neutral species abundance distributions (SADs) for SADs resulting from simulations of our niche model (solid lines) and for the distributions predicted by the model of Chisholm and Pacala (dashed lines), for the 5-, 20-, and 50-niche cases with  $\rho = 4$ . Shown are the differences in the mean proportion of species in the community in logarithmically scaled abundance classes, with those classes delineated as in Volkov et al. (2003) and as in the main text.



Appendix Figure S6: Stem plots for five-niche communities with restricted trait ranges. a) 1/4 trait span: each niche spans an interval of size 0.5, which is 1/4 the size of the full range. b) 1/2 trait span: each niche spans an interval size of 0.1, which is 1/2 the size of the full range.



Appendix Figure S7: Average competition strength and abundances within a single niche in a 5-niche community ( $\rho = 4$ ), showing that the trend in total competition strength is dominated by the trend in between-niche competition, and that abundance is maximized where both total and between-niche competition are minimized. (a) Relative strength of outside and within-niche competition. A fixed set of equally spaced traits  $u_i = 1...S_n$ , where  $S_n$  is the average number of species within a niche, is used as a test set on which to compute outside and within-niche competition from existing species. The test set is placed in the centermost niche of each final simulation configuration for consistency, and competition strength from existing outside and inside species is averaged over 1000 simulation configurations. (b) Average abundance across a single niche. Abundances from each of five niches over 1000 simulations are binned and averaged.