FORUM

On testing the role of niche differences in stabilizing coexistence

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Summary

Replacement series designs have been criticized because they may inaccurately predict the outcome of competition, particularly when species' vital rates respond to competitor density in strongly nonlinear ways. Here we explain that despite this concern, experiments manipulating frequency can still effectively quantify the strength of niche differences in stabilizing coexistence, the goal of an experiment we proposed in an earlier paper. Niche differences cause species to have greater per capita growth rates when rare than when common, and we demonstrate that this result is robust to variation in total density. We also emphasize that our proposed experimental design does not call for fixing density across species' frequency gradients, thus differing from a traditional replacement series design. We show that our approach and the more labor-intensive response surface design share the same theoretical foundation and both are apppropriate for quantifying the role of niche differences in stabilizing the dynamics of coexisting species.

Coexistence occurs when the stabilizing effects of niche differences exceed fitness differences between species (Chesson 2000). Niche differences cause species to limit themselves more than they limit their competitors, resulting in higher per capita growth rates when species are rare than when they are common – negative frequency dependent growth (Fig. 1). Fitness differences, by contrast, drive competitive exclusion, and thus make coexistence harder to achieve. The neutral theory (Hubbell 2001) is the special case with no niche or fitness differences. In Adler, Hille Ris Lambers & Levine (2007), we proposed several analyses to determine whether the observed coexistence in a particular community results from strong niche differences exceeding large fitness differences or weak niche differences overcoming small fitness differences. In the first of these analyses, we suggested quantifying the stabilizing influence of niche differences by measuring negative frequency dependence in species' per capita growth rates.

In his forum paper, Damgaard (2008) objects to the experimental approach Adler *et al*. proposed for identifying the strength of niche differences. He argues that because of nonlinear responses of species' vital rates to density, both density and frequency need to be manipulated, resulting in what is commonly called a 'response surface' design (Law & Watkinson 1987; Joliffe 2000; Inouye 2001). We agree with Damgaard that, in theory, strong nonlinearities in how vital rates respond to density could cause the predicted outcome

of competition to change with the fixed total density of a substitution experiment. However, because Damgaard misinterprets the goals of our experiment and the recommended methodology, his concerns with our approach are misplaced.

Here we first clarify the experiment outlined in Adler *et al*. 2007, demonstrating that it quantifies the role of niche differences in stabilizing coexistence in a theoretically sound manner. We emphasize that density is not fixed across the frequency gradient, and that the design shares the identical theoretical justification as the response surface experiment advocated by Damgaard (2008). Second, we show that our approach is robust to inaccuracies in planting density. We stress that the goal of our proposed experimental approach is not predicting the qualitative outcome of competition (coexistence or exclusion), as Damgaard implies, but rather quantifying the role of niche differences in stabilizing the dynamics of species already observed to co-exist.

We explain the theoretical justification for our experiment and the response surface design advocated by Damgaard and others (Law & Watkinson 1987; Joliffe 2000; Inouye 2001) with a phase plane analysis. Many models of competing species, including those in Adler *et al*. (2007), Damgaard (2008), and the Lotka-Volterra models produce linear zero growth isoclines, as in Fig. 1a. Coexistence occurs when these isoclines cross so that each species experiences positive growth rates when rare. In response surface experiments, two species are planted across a wide range of both frequency and density in order to cover the entire phase space shown in

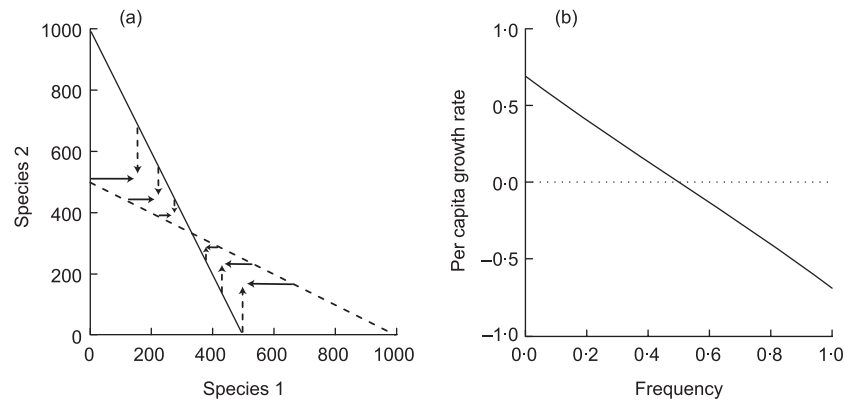*Correspondence author. E-mail: levine@lifesci.ucsb.edu

Fig. 1. (a) Zero growth isoclines for two competing species. Growth is positive between the origin and the isocline. Solid lines correspond to species 1 and dashed lines for species 2. Arrows indicate the relative size and sign of species per capita growth rates at various locations along the isocline of their competitor. Notice that these arrows predict the convergence of the system to the equilibrium point. In (b) the per capita growth rates of species 1 (represented by the solid arrows in (a)) are plotted against its frequency. The negative slope reflects the strength of niche differences in the system- species limit themselves more than their competitors. The plots were produced by setting $\beta_1 = \beta_2 = 0 \cdot 0002$, $\alpha_1 = \alpha_2 = 0 \cdot 0002$, $c_{12} = c_{21} = 0 \cdot 5$, $p_1 = p_2 = 0 \cdot 1$, $\theta_1 = \theta_2 = \phi_1 = \phi_2 = 1$ in the model in Damgaard (2008), which is equivalent to the model in Adler *et al.* 2007 when $\lambda_1 = \lambda_2 = 500$, $\alpha_{11} = \alpha_{22} = 1$, $\alpha_{12} = \alpha_{21} = 0 \cdot 5$.
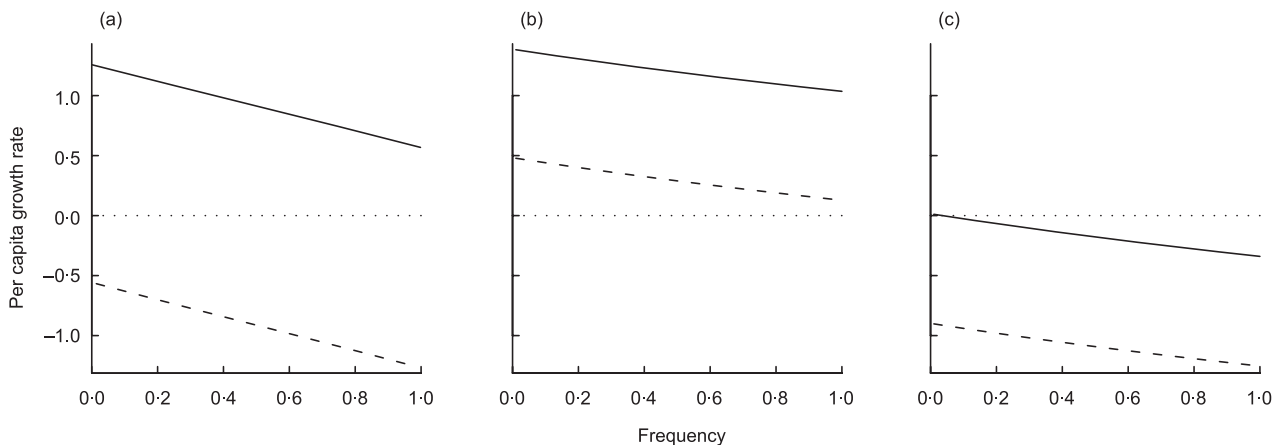

Fig. 2. The relationship between per capita growth rate and frequency following the population model in Damgaard (2008), using the parameters of his Fig. 1. In (a), we conduct the proper 'experiment' following Adler *et al.* 2007. We varied the density of each focal species from near zero to its single species carrying capacity or greater. At each density, the resident competitor was allowed to equilibrate in response to the abundance of the focal species, creating a fully saturated system ($x_i = u_i - c_{ij}x_j$ defines species *i*'s zero growth isocline, with terms defined in Damgaard 2008). We then used Damgaard's equation 2 to calculate the growth rate (log of the proportional change in density between years) of the focal species across the range of densities, and converted those densities into units of frequency. In (b) and (c), we conducted the experiment at a *fixed* total densities too low (175 individuals, half the two species average carrying capacity of 350 individuals) and too high (700 individuals) for the system. In all three panels, the niche difference between the species (the fact that on average, intraspecific effects are stronger than interspecific effects in Damgaard's model) are reflected in the negative slopes between per capita growth rate and frequency. In a neutral model, the lines would be perfectly horizontal and lie directly upon one another (Adler *et al.* 2007).

Fig. 1a. Next, growth rates, or some proxy, are measured at each density combination. Finally, the growth vectors are mapped on the phase plane to identify each species' zero growth isocline, and examine the behaviour of the system around those isoclines. Although this approach does not require a priori knowledge about the equilibrium densities of the two competing species, the highest and lowest densities used must bracket the equilibria.

The experiment we proposed to quantify negative frequency-dependent growth (and produce Fig. 2 in Adler *et al.* 2007) simply uses a subset of the density combinations from the same phase plane. In particular, we take advantage of the fact that species growth rates around the zero growth isoclines predict coexistence dynamics (Fig. 1). Thus, we vary the density

of a focal species, but at each density we allow the resident species (or community in a many species system) to equilibrate in response to the focal species' density (Adler *et al.* 2007). The purpose of this latter step is to place the community on the zero growth isocline (Fig. 1a). Our approach is not a substitution design as Damgaard implies, because the total density of the community is not fixed across the frequency treatments.

For example, to quantify negative frequency-dependent growth for species 1 in Fig. 1, we would first establish a community with one individual of species 1. Species 2 would be planted into this community at the density it eventually reaches in a system with a single individual of its competitor. Of course, this is the density of species 2 on its zero growth isocline (Fig. 1a) when species 1 has one individual (how one

empirically determines this density and the consequences of inaccuracies are discussed below). We then repeat these steps to establish communities with increasing densities of species 1. Lastly, after measuring the per capita growth rate of species 1 at each density combination, this rate is plotted against its frequency in each planted community (Fig. 1b). The stronger the niche differences, the steeper the slope, and the more stabilized is the coexistence.

In theory, nonlinearities could cause species relative performance to differ at density combinations far away from the isoclines (not explored in our experiment), but community behaviour at such densities does not determine coexistence. Moreover, we are aware of no empirically demonstrated forms of nonlinear density-dependence that change our interpretation of this experiment; we are simply arguing that niche differences give competing species advantages when rare versus common. The model in Damgaard (2008) is entirely consistent with our approach. It produces linear zero growth isoclines as in Fig. 1a ($x_i = u_i - c_{ij}x_j$ defines species i's isocline, with terms defined in Damgaard 2008). When we conduct the Adler *et al.* experiment using Damgaard's (2008) parameterized model, it correctly predicts the coexistence outcome (Fig. 2a): despite negative frequency dependence, the inferior species has a negative growth rate when rare, and is competitively excluded (as in Fig. 1a of Damgaard 2008).

In sum, the response surface and Adler *et al.* designs are both justified by the same theory, and both can be used to investigate niche differences, as shown in Fig. 1b. It is simply up to the investigator to decide which is more feasible. While the traditional response surface solution requires at least several times the planting combinations of our design, the latter requires some prior knowledge about equilibrium densities of the competitors (e.g. the zero growth isoclines) or time for the resident species to equilibrate to the planted densities of the focal species. For this latter reason, Adler *et al.* (2007) recommended our approach for short-lived species such as annual plants. If this proves too challenging, an alternative is to use the statistical approaches we outlined for analysing natural spatial or temporal gradients in commonness and rarity.

Because predicting the equilibrium densities of competitors is difficult, it is important to consider how sensitive the experimental results are to inaccuracies in planting density. In addition, how different would the conclusions be if the experiment were conducted at a *fixed* total density or seed mass approximating the natural community (e.g. Harpole & Suding 2007)? If our goal was to predict coexistence, errors in planting density would be important because small changes in growth rates when rare can mean the difference between coexistence and exclusion (Chesson 2000). For example, Damgaard's Fig. 1 illustrates an experiment where the competitively inferior invader has a positive growth rate when rare, but only because the resident competitor was planted at one fifth its carrying capacity. Not surprisingly, the experiment yields a false prediction for coexistence.

However, if the goal of the experiment were to assess the strength of niche differences in driving coexistence, errors in planting density are far less important. The experiment Adler *et al.* (2007) propose begins with the premise that the focal species co-occur, and that the strength of niche differences in driving coexistence is quantified by the slope of the line relating each species' per capita growth rate to its frequency in the community (Fig. 1b). This slope is far more robust to errors in planting density than the qualitative outcome of competition (whether per capita growth rates when rare are positive or negative). We demonstrate this point by using Damgaard's model to conduct hypothetical experiments at fixed total densities too low and too high for the system (Fig. 2b,c). In all cases, the influence of niche differences on coexistence is shown by the negative relationship between frequency and per capita growth rate.

An important point is that these hypothetical experiments (Fig. 2b,c) were conducted at *fixed* total densities. Thus if investigators have reasonable knowledge of natural densities of their plant community, and conduct a replacement series (substitution) design near that density, the slope of the line relating per capita growth rate to frequency relates to the strength of niche differences. This result is consistent with past empirical findings that the outcome of competition in replacement series designs does not change with density as long as the community nears its asymptotic biomass (Taylor & Aarssen 1989; Cousens & O'Neill 1993). While response surface experiments are necessary for evaluating the behaviour of systems at less than their asymptotic natural densities and for estimating competition coefficients (Joliffe 2000; Inouye 2001), neither is a goal of our experimental analysis.

In sum, we hope to have clarified two equally justified approaches for assessing of the role of niche differences in stabilizing coexistence.

Acknowledgements

References

Adler, P.B., Hille Ris Lambers, J. & Levine, J.M. (2007) A niche for neutrality. *Ecology Letters*, **10**, 95–104.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Cousens, R. & O'Neill, M. (1993) Density dependence of replacement series experiments. *Oikos*, **66**, 347–352.

Damgaard, C. (2008) On the need for manipulating density in competition experiments. *Functional Ecology*, **22**, doi: 10.1111/j.1365-2435.2008.01456.x

Harpole, W.S. & Suding, K.N. (2007) Frequency-dependence stabilizes competitive interactions among four annual plants. *Ecology Letters*, **10**, 1164–1169

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.

Inouye, B.D. (2001) Response surface experimental designs for investigating interspecific competition. *Ecology*, **82**, 2696–2706.

Joliffe, P.A. (2000) The replacement series. *Journal of Ecology*, **88**, 371–385.

Law, R. & Watkinson, A.R. (1987) Response-surface analysis of two species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. *Journal of Ecology*, **75**, 871–886.

Taylor, D.R. & Aarssen, L.W. (1989) On the density dependence of replacement-series competition experiments. *Journal of Ecology*, **77**, 975–988.