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 appropriate 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) 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

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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 \( \beta_1 = \beta_2 = 0.0002, \alpha_1 = \alpha_2 = 0.0002, c_{12} = c_{21} = 0.5, p_1 = p_2 = 0.1, \theta_1 = \theta_2 = 0.1, \phi_1 = \phi_2 = 1 \) in the model in Damgaard (2008), which is equivalent to the model in Adler et al. 2007 when \( \lambda_1 = \lambda_2 = 500, \alpha_{11} = \alpha_{22} = 1, \alpha_{12} = \alpha_{21} = 0.5 \).

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).
isoclines as in Fig. 1a (consistent with our approach. It produces linear zero growth versus common. The model in Damgaard (2008) is entirely
pretation of this experiment; we are simply arguing that niche
forms of nonlinear density-dependence that change our inter-
behaviour at such densities does not determine coexistence.
Moreover, we are aware of no empirically demonstrated forms of nonlinear density-dependence that change our inter-
pretation 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 \( (x_i = u - c_i x) \), 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 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; Coussens & 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.

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