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Disentangling the effects of external perturbations on coexistence and priority effects

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Abstract

1. A major challenge in ecological research is to identify the tolerance of ecological communities to external perturbations. Modern coexistence theory (MCT) has been widely adopted as a framework to investigate the tolerance to perturbations in relative reductions of per capita growth rates, often using metrics that explicitly eliminate the independent role of intrinsic growth rates. More recently, the structural approach (SA) was introduced to investigate the tolerance of communities to perturbations in intrinsic growth rates as a function of the strength of intraspecific and interspecific competition. Because the external perturbations are likely to happen in both intrinsic growth rates and competition strengths, no framework alone can fully disentangle the effects of external perturbations.

2. Here we combine MCT and SA to disentangle the tolerance in coexistence and priority effects of a pair of competing species when subject to perturbations in intrinsic growth rates and competition strengths. Through this combination, we reveal the emergence of a key trade-off: increasing the tolerance to perturbations in intrinsic growth rates typically decreases the tolerance in competition strengths, and vice versa. Furthermore, this trade-off is stronger under coexistence than under priority effects.

3. We test this combined framework on competing pairs of 18 California annual plant species. For both coexistence and priority effects, we find that the tolerance to perturbations in intrinsic growth rates is maximized instead of that to perturbations in competition strengths in the studied annual plant communities.

4. *Synthesis.* Our combined framework of modern coexistence theory and structural approach illustrates that it is possible to disentangle the impact of different external perturbations on the persistence of species. Importantly, our findings show that species interactions may reveal whether communities are dominated either by changes in intrinsic growth rates or by competition strengths. Overall, this combined framework can open a new perspective to understand and predict the response of populations to changing environmental conditions.

KEYWORDS
coexistence, competition strengths, intrinsic growth rates, modern coexistence theory, priority effects, structural approach, tolerance to perturbations

1 | INTRODUCTION

Understanding the conditions leading to species coexistence and priority effects has long been a central research topic in community ecology (Fukami, 2015; Levine, Bascompte, Adler, & Allesina, 2017; Morin, 2009; Vellend, 2016). Coexistence occurs when multiple species persist within the same location for a continuous period of time (Case, 2000; Hofbauer & Sigmund, 1998). In contrast, priority effects occur when the dynamics of the community are governed by the order of species arrivals (Chase, 2003; Fukami, 2015; Song, Altermatt, Pearse, & Saavedra, 2018). The majority of theoretical studies have addressed this topic by focusing on the necessary and/ or sufficient conditions compatible with coexistence or priority effects assuming that model parameters (e.g. intrinsic growth rates and competition strengths) are fixed (Barabás, D'Andrea, & Stump, 2018; but see Vandermeer, 1975). Nonetheless, model parameters (either mechanistic or phenomenological) change in response to unavoidable external perturbations (Dirzo et al., 2014; Levins, 1968; Scheffers et al., 2016; Tucker & Fukami, 2014), leading to the natural question of how robust coexistence and priority effects are to changes in model parameters. Our ability to address this question has been shaped by two different frameworks—modern coexistence theory (MCT; Chesson, 2018) and the structural approach (SA; Saavedra, Rohr, et al., 2017).

Modern coexistence theory (Chesson, 2000, 2018) has been widely adopted as a framework to investigate the conditions leading to species coexistence and has more recently been extended to priority effects (Fukami, Mordecai, & Ostling, 2016; Grainger, Letten, Gilbert, & Fukami, 2019; Ke & Letten, 2018; Levine & HilleRisLambers, 2009; Mordecai, Molinari, Stahlheber, Gross, & D'Antonio, 2015). In particular, MCT shows that coexistence occurs when the effects of niche overlap exceed the effects of biasing the fitness ratio on the inferior species. Likewise, MCT has shown that priority effects occur when the effects of destabilizing mechanisms (such as positive frequency dependence) exceed the effects of biasing the fitness ratio for the superior competitor (Ke & Letten, 2018; Schreiber, Yamamichi, & Strauss, 2019). Importantly, MCT allows us to understand the robustness of coexistence to random perturbations in relative reductions in per capita growth rates (Barabás et al., 2018). A pair of competitors can be located in the parameter space (of relative reductions in per capita growth rate) relative to the boundary between coexistence and exclusion. The further into the coexistence region a pair lies, the more robust coexistence would be to changes in the average fitness or niche overlap of the competitors. Analogous predictions can be made for priority effects. Yet, the metrics in MCT (such as niche overlap and fitness ratio) are often calculated based on competition coefficients scaled by intrinsic growth rates, which explicitly eliminate the independent role of intrinsic growth rates (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Pérez-Ramos, Matías, Gómez-Aparicio, & Godoy, 2019).

More recently, the SA (Saavedra, Rohr, et al., 2017) was introduced to investigate the range of intrinsic growth rates compatible with coexistence and priority effects, as a function of the absolute reductions in per capita growth rate (a.k.a. competition strengths; Cenci, Song, & Saavedra, 2018). The region of coexistence is described by an angle anchored at the origin of a plot whose *x* and *y* axes are the intrinsic growth rates of the two competitors. The wider the angle, the greater the range of intrinsic growth rate differences between competitors compatible with coexistence. The angle becomes a solid angle or cone in a higher dimension for communities containing more than two competitors (Song, Rohr, & Saavedra, 2018). In this way, SA is specifically designed to understand the robustness of a community—as a function of competition strengths—to random changes in the intrinsic growth rates of the constituent species.

Because external perturbations are likely to happen in both the intrinsic growth rates and competition strengths (either simultaneously or separately), here we argue for a combination of MCT and SA focused on parameter changes (perturbations). SA and MCT measure different aspects of the robustness of coexistence (priority effects): SA has thus far been developed with only perturbations to the intrinsic growth rates in mind (the robustness as a function of competition strengths); MCT has been developed with the idea of potential simultaneous changes in parameters, but merging them into a single parameter (relative reductions in per capita growth rate). Note that intrinsic growth rates and competition strengths are phenomenological summaries of different abiotic and biotic factors (Cadotte & Tucker, 2017; Coulson et al., 2017; Levins, 1968; MacArthur, 1970), and they play different fundamental roles in shaping the dynamics of multispecies systems (Cenci & Saavedra, 2018; Song & Saavedra, 2018a, 2018b). Therefore, achieving a combination of MCT and SA is challenging because the metrics in the two approaches are not directly translatable (appendix S5 in Saavedra, Rohr, et al., 2017). Yet, instead of translating their metrics, we propose to investigate how the angle describing the intrinsic growth rates compatible with coexistence (priority effects) in SA changes as a function of the niche overlap and fitness ratio in MCT.

Our combination of MCT and SA focuses on two-species competition dynamics. While SA can be used for two-species and multispecies communities within the same formalism (Saavedra, Rohr, et al., 2017), here we focus on two-species dynamics given that the canonical formalism of MCT is explicitly justified for two-competing species (Barabás et al., 2018; Chesson, 2018; Song, Barabás, & Saavedra, 2019; Spaak & DeLaender, 2018). Note that MCT can also be applied to multispecies communities, but the formalism and definitions are different (Barabás et al., 2018; Song et al., 2019). Nevertheless, the results obtained for two-species communities are valuable for both theoretical and empirical research (Case, 2000). From a theoretical perspective, the combination of MCT and SA not only could allow us to disentangle the role played by intrinsic growth rates and competition strengths in shaping coexistence and priority effects but also could offer a new perspective to understand the tolerance of ecological communities to the effects of simultaneous external perturbations on different model parameters. From an empirical perspective, because two-species dynamics has been and continues to represent the most feasible experimental system

(Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Bimler, Stouffer, Lai, & Mayfield, 2018; Cardinaux, Hart, & Alexander, 2018; Chu et al., 2016; Germain, Mayfield, & Gilbert, 2018; Godoy, Kraft, & Levine, 2014; Grainger et al., 2019; Kraft, Godoy, & Levine, 2015; Levine & HilleRisLambers, 2009; Li, Tan, Yang, Ma, & Jiang, 2018; Mayfield & Levine, 2010; Mordecai et al., 2015; Narwani, Alexandrou, Oakley, Carroll, & Cardinale, 2013; Pérez-Ramos et al., 2019), this combination of theoretical tools can be easily applied to gain new insights about the robustness of ecological communities to changing environmental conditions.

The manuscript is organized as follows. First, building upon two-competing species dynamics, we briefly introduce the fundamentals of MCT and SA. We show why each framework alone cannot fully disentangle the roles played by intrinsic growth rates and competition strengths. Then, we show how the metrics from MCT—the stabilizing and equalizing mechanisms—relate to the solid angle of SA. Achieving this combination of tools requires both advancing SA to simultaneously vary multiple parameters (as in MCT) and revisiting MCT to untangle the contribution of model parameters (as in SA). Importantly, we show that the equalizing mechanism (based on fitness ratio) exhibits a key trade-off between tolerance to perturbations in intrinsic growth rates and in competition strength. We show that this trade-off is stronger under coexistence than under priority effects. Next, we apply our study to an empirical dataset of annual plant assemblages. We show that in these experimental systems, the tolerance to perturbations in intrinsic growth rates (but not in competition strengths) is maximized. Last, we provide a discussion about the limitations and future research avenues derived from our work.

2 | TWO-COMPETING SPECIES DYNAMICS

2.1 | Dynamics

Many population dynamics of two-competing species have been proposed (e.g. Case, 1999; Tilman, 1982; Turchin, 2003). Arguably, the simplest dynamics is the classic Lotka–Volterra (LV) dynamics (Case, 1999). The formulation of LV reads as (other equivalent parameterizations or formalisms can be found in Appendix S1).

$$\begin{cases} \frac{dN_1}{dt} = N_1(r_1 - \alpha_{11}N_1 - \alpha_{12}N_2) \\ \frac{dN_2}{dt} = N_2(r_2 - \alpha_{21}N_1 - \alpha_{22}N_2), \end{cases} \qquad (1)$$

where the variable N_i represents the abundance of species i, the parameters $r_i > 0$ and $\alpha_{ii} > 0$ correspond to the intrinsic growth rate and the self-regulation (or intraspecific competition) of species i, respectively, and $\alpha_{12} > 0$ and $\alpha_{21} > 0$ are the corresponding interspecific competition strengths (a.k.a. absolute reductions in per capita growth rate).

Importantly, despite the simplicity of LV dynamics, all the main results here apply to a much larger class of two-competing species dynamics, including saturating competition dynamics (Brauer &

Castillo-Chavez, 2011), time discrete LV dynamics (Saavedra, Rohr, et al., 2017), consumer-resource dynamics (Letten, Dhami, Ke, & Fukami, 2018; Song et al., 2019) and annual plant dynamics (Godoy & Levine, 2014; Hart, Turcotte, & Levine, 2019). Note that the strength of species competition in these dynamics can also be expressed in terms of nonlinear functional responses (Cenci & Saavedra, 2018).

2.2 | Coexistence

The necessary and sufficient conditions for the coexistence of the two competing species are given by the two following inequalities (Song & Saavedra, 2018b; Vandermeer, 1975):

$$\frac{\alpha_{21}}{\alpha_{11}} < \frac{r_2}{r_1} < \frac{\alpha_{22}}{\alpha_{12}}. \qquad (2)$$

The two inequalities, $\alpha_{21}/\alpha_{11} < r_2/r_1$ and $r_2/r_1 < \alpha_{22}/\alpha_{12}$, grant that species 1 and 2 can mutually invade given r_2/r_1—what we call the ratio of intrinsic growth rates. In a two-dimensional system, this possibility grants that species can have positive abundance at equilibrium, viz. *feasibility* (Case, 2000). Consequently, these two inequalities imply the third inequality $\alpha_{21}/\alpha_{11} < \alpha_{22}/\alpha_{12}$, which ensures that the dynamics would converge to the equilibrium starting from any initial species abundance, viz. *global stability*. Note that the third inequality can be deduced from the first two inequalities, but the inverse is not true. Because these conditions guarantee the existence of a unique, stable, feasible, fixed point, species coexistence is not determined by the order of species arrival.

Traditionally, these inequalities have been graphically illustrated on the state (abundance) space of the system given by Equation 1 (Case, 2000). Following this classic representation, Figure 1 shows how the parameters have to be combined such that the two non-trivial zero-growth isoclines fall inside the coexistence area. For given generic values of $K_1 = r_1/\alpha_{11}$ and $K_2 = r_2/\alpha_{22}$—known as carrying capacities, the inequality $r_2/r_1 < \alpha_{22}/\alpha_{12}$ is equivalent to having species 1 zero-growth isocline crossing the N_2 axis above species 2 zero-growth isocline, and similarly for the inequality $\alpha_{21}/\alpha_{11} < r_2/r_1$. The global stability condition $\alpha_{21}/\alpha_{11} < \alpha_{22}/\alpha_{12}$ is equivalent to having the slope of species 1 zero-growth isocline steeper than the one of species 2 so that they cross within the coexistence area (Case, 2000). Note that the borders on the axes of Figure 1 (as well as the region where the two zero-growth isoclines would cross outside the positive abundances quadrant) correspond to the case of unfeasible equilibria, where one species out-competes the other species—also known as border equilibria. Pure neutrality lies in the intersection between the stability–instability border and the fitness equivalence line (Song et al., 2019).

2.3 | Priority effects

Figure 1 also shows how the parameters should be combined such that the dynamics exhibit priority effects (Case, 2000). Recall that