

RESEARCH ARTICLE

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).

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

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, Dhimi, 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):

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

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

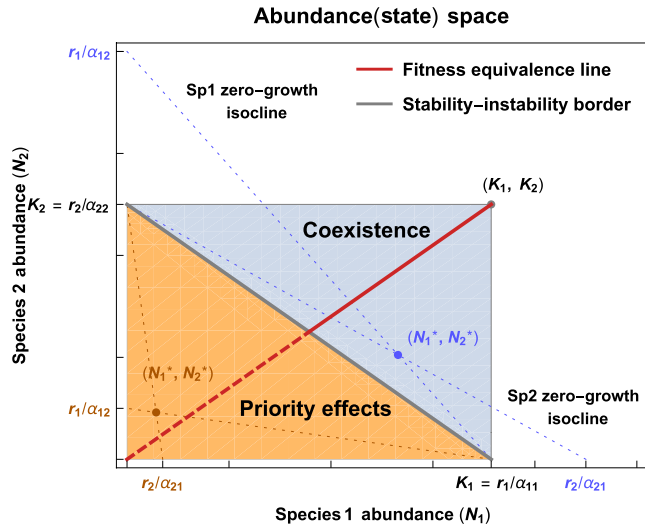


FIGURE 1 Coexistence and priority effects. State (abundance) space of two-competing species. Species 1 zero-growth isocline is defined as $r_1 = \alpha_{11}N_1 + \alpha_{12}N_2$, and its slope corresponds to $-\alpha_{11}/\alpha_{12}$. We can write a symmetric equation for species 2. These isoclines (dotted lines) correspond to the non-trivial set of abundances where species per capita growth rate is zero. The intersection of these two isoclines defines an equilibrium point (N_1^*, N_2^*) . The carrying capacity $K_i = r_i/\alpha_{ij}$ is the abundance that species i reaches when the competition strength is zero ($\alpha_{ij} = 0$). Within the state space, we can define the coexistence area (top blue region) and the priority-effect area (bottom orange region). That is, keeping the carrying capacities fixed, depending on where the two isoclines cross, the two species can either exhibit coexistence or priority effects. Note that the grey line divides the region of stability (top region) and instability (bottom region). The red line represents the fitness equivalence line, and in dashed, its extension to priority effects

priority effects in a two-species LV system correspond to the ecological case when the first arriving species (assumed to be at its carrying capacity) always excludes the second arriving species that tries to invade (considered to have lower abundance)—due to the instability of the feasible fixed point. Mathematically, priority effects are equivalent to the existence of a feasible but unstable equilibrium point in this system. Thus, the necessary and sufficient conditions to have priority effects are the opposite of the coexistence inequalities (Equation 2):

$$\frac{\alpha_{21}}{\alpha_{11}} > \frac{r_2}{r_1} > \frac{\alpha_{22}}{\alpha_{12}}. \quad (3)$$

Similar to the coexistence case, we can geometrically interpret these priority effects inequalities as follows. The inequality $\alpha_{21}/\alpha_{11} > r_2/r_1$ is equivalent to have species 1 zero-growth isocline crossing the N_2 axis below species 2 zero-growth isoclines, and similarly for $r_2/r_1 > \alpha_{22}/\alpha_{12}$. In turn, the dynamical instability condition $\alpha_{21}/\alpha_{11} > \alpha_{22}/\alpha_{12}$ is equivalent to have the slope of species 2 zero-growth isocline steeper than that of species 1—such that they cross within the priority effects area. Note that there is a feasible equilibrium point (i.e. the isoclines cross inside the

positive quadrant of species abundances), but the equilibrium point is unstable.

3 | MODERN COEXISTENCE THEORY

3.1 | Coexistence

To investigate the conditions leading to species coexistence, MCT (Chesson, 2013) has reformulated the classic two-species LV competition system (Equation 1) as,

$$\begin{cases} \frac{dN_1}{dt} = N_1 r_1 (1 - \bar{\alpha}_{11} N_1 - \bar{\alpha}_{12} N_2) \\ \frac{dN_2}{dt} = N_2 r_2 (1 - \bar{\alpha}_{21} N_1 - \bar{\alpha}_{22} N_2). \end{cases} \quad (4)$$

In Equation 4, the intrinsic growth rates r_i (dimension: time^{-1}) are the same as the ones in Equation 1. However, the *relative competition strength* $\bar{\alpha}_{ij}$ (dimension: biomass^{-1} or abundance^{-1}) is different from α_{ij} (dimension: $\text{time}^{-1} \cdot \text{biomass}^{-1}$ or $\text{time}^{-1} \cdot \text{abundance}^{-1}$). Here, $\bar{\alpha}_{ij}$ represents the per capita effect of species j on the per capita growth rate of species i relative to its intrinsic growth rate (i.e. reductions in per capita growth rate relative to the maximum per capita growth rate). In other words, $\bar{\alpha}_{ij}$ and α_{ij} represent the relative and absolute reductions in per capita growth rate, respectively. These parameters are related by the formula $\bar{\alpha}_{ij} = \alpha_{ij}/r_i$.

Note that mixing up these two parameterizations above (both are equally called competition strengths in the literature) can lead to apparently contradictory results. For instance, MCT states that two competing species will coexist as long as the species depress their own growth more strongly than they depress the growth of the other species, which can be interpreted as $\alpha_{ii} > \alpha_{ji}$ (Chesson, 2013, 2018). However, if one considers $r_1 = 1$ and $r_2 = 2$, Equation 2 becomes $\alpha_{21}/\alpha_{11} > 1/2$, and $\alpha_{12}/\alpha_{22} > 2$, in which case, species 1 can depress its own growth *less* strongly than it depresses the growth of the other species, and yet both species can coexist. The statement of MCT holds only for the relative reductions in per capita growth rate defined by $\bar{\alpha}_{ij}$, that is, $\bar{\alpha}_{ii} > \bar{\alpha}_{ji}$, which embed the intrinsic growth rate into the competition strength. Similarly, it has been stated that the role of intrinsic growth rates in coexistence does not appear to be fundamental (Chesson, 2018). However, it can be proved that $\bar{\alpha}_{ij}$ are not sufficient to determine the dynamical behaviour beyond two-species population dynamics (Poincaré-Bendixson theorem: Strogatz, 2014; see Appendix S2 for a detailed discussion).

Then, under MCT, the coexistence criteria (Equation 2) for a two-species LV competition system are given by

$$\rho < \sqrt{\frac{\bar{\alpha}_{11}\bar{\alpha}_{12}}{\bar{\alpha}_{22}\bar{\alpha}_{21}}} < \frac{1}{\rho}, \quad (5)$$

where $\rho = \sqrt{\bar{\alpha}_{12}\bar{\alpha}_{21}/\bar{\alpha}_{11}\bar{\alpha}_{22}} = \sqrt{\alpha_{12}\alpha_{21}/\alpha_{11}\alpha_{22}}$ is called the *niche overlap*, and $\sqrt{\bar{\alpha}_{11}\bar{\alpha}_{12}/\bar{\alpha}_{22}\bar{\alpha}_{21}}$ is called the *fitness ratio* (Bartomeus & Godoy, 2018; Chesson, 2018). Note again that the fitness ratio apparently

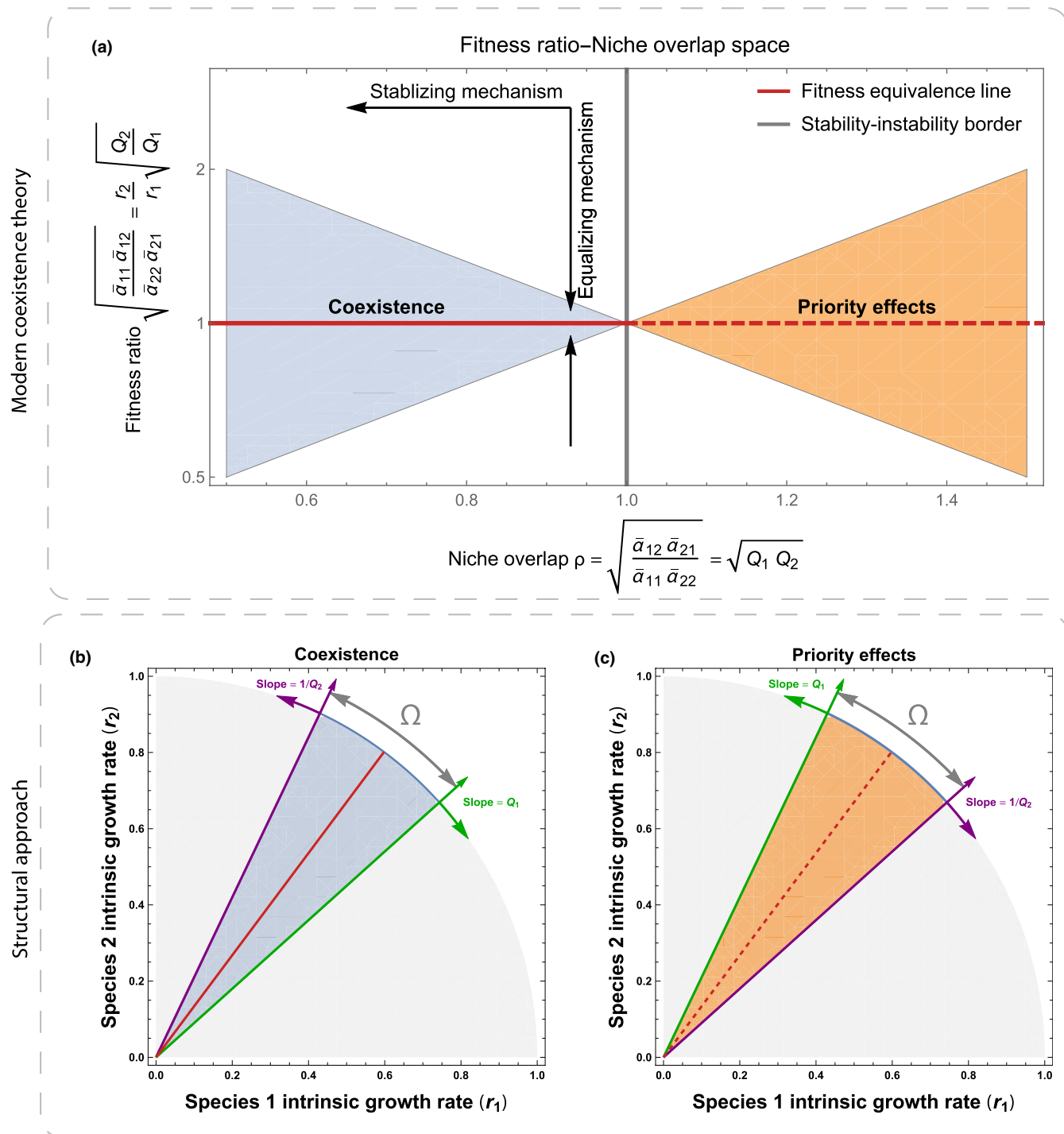


FIGURE 2 Modern coexistence theory (MCT) and the structural approach (SA). The dynamics correspond to the Lotka–Volterra model (Equation 1). (a) MCT. Fitness ratio and niche overlap space for coexistence and priority effects. The figure represents the four different outcomes of the dynamical system as a function of the fitness ratio and niche overlap (fitness ratio is on log ratio). The vertical red line is the border between the stability–instability area ($\rho = 1$). The coexistence area is deduced from the inequalities in Equation 5 (i.e. Equation 8), while priority effects are deduced from the inequalities in Equation 6. The arrows illustrate the direction in which the competition strengths need to move inside the fitness ratio and niche overlap space to act as stabilizing and equalizing mechanisms. The grey line represents the stability–instability border. (b, c) SA. Quantifying structural stability of coexistence and priority effects under perturbations in intrinsic growth rates. For a competition system, the full effective space of intrinsic growth rates is the quarter unit circle in the positive quadrant (Song, Rohr, et al., 2018), which is depicted in grey. The blue (orange) area corresponds to the domain of coexistence (priority effects) within the effective parameter space, as defined by Equations 2 and 3. Note that the two borders (depicted as purple and green lines) switch between coexistence and priority effects. The feasibility domain (normalized solid angle) Ω is defined as the angle between the two borders. The region Ω can be increased as the borders move along with the directions of arrows. The red line represents the fitness equivalence line, and in dashed, its extension to priority effects

does not depend on the intrinsic growth rates r_i , but recall that they are implicitly embedded into $\bar{\alpha}_{ij}$. Hence, the stability condition for stable coexistence is equivalent to $\rho < 1$.

Consequently, MCT identifies two ecological mechanisms under which two species can achieve coexistence: the equalizing mechanism ($\sqrt{\bar{\alpha}_{11}\bar{\alpha}_{12}/\bar{\alpha}_{22}\bar{\alpha}_{21}}$ approaches 1) and the stabilizing mechanism (ρ approaches 0). The stabilizing mechanism increases the range of fitness ratios leading to coexistence, while the equalizing mechanism tends to *centre* the fitness ratio within the given range of niche overlap. Typically, these inequalities are represented by the blue area within the two-dimensional space made by the niche overlap and the fitness ratio axes (Figure 2a). Hence, the stabilizing mechanism can be seen on this fitness ratio–niche overlap space as horizontal trajectories towards the left inside the coexistence area. In turn, the equalizing mechanism can be seen as vertical trajectories in the direction of the fitness equivalence line inside the coexistence area. Note, however, that changes in niche overlap are likely to restrict changes (of both direction and magnitude) in fitness ratio, and vice versa (Song et al., 2019).

3.2 | Priority effects

Importantly, the concepts of niche overlap and fitness ratio can be naturally extended to study priority effects (Ke & Letten, 2018). Indeed, the inequalities shown in Equation 3 can also be read as

$$\rho > \sqrt{\frac{\bar{\alpha}_{11}\bar{\alpha}_{12}}{\bar{\alpha}_{22}\bar{\alpha}_{21}}} > \frac{1}{\rho}. \quad (6)$$

Note that in the priority effects case, the niche overlap has to be larger than 1, that is, $\rho > 1$. Consequently, the definition of niche overlap (and the stabilizing mechanism) can be extended to priority effects, but its interpretation is the opposite as in the coexistence case, that is, ρ has to be as large as possible to accommodate a larger magnitude of fitness ratio leading to priority effects. Figure 2a shows the fitness ratio–niche overlap space for priority effects. Note that the interpretation of the equalizing mechanism remains the same as in the coexistence case, that is, the mechanism centres the fitness ratio within the range given by the niche overlap (Ke & Letten, 2018).

4 | STRUCTURAL APPROACH

Different from MCT, SA follows the classic formulation of the LV model and focuses on the region of intrinsic growth rates compatible with species coexistence as a function of competition strengths (a.k.a. absolute reductions in per capita growth rate; Saavedra, Rohr, et al., 2017). That is, SA studies to what extent the intrinsic growth rates (r_i) can change given the competition strengths (α_{ij}) that are usually considered as being fixed (but see Cenci, Montero-Castaño, & Saavedra, 2018; Saavedra, Cenci, Val, Boege, & Rohr, 2017 for the application of SA to changing competition strengths). Following this approach, the region of the ratio

of intrinsic growth rates (r_2/r_1) compatible with species coexistence and priority effects of two species is analytically described by Equations 2 and 3 respectively. This region, known as the feasibility domain, can be geometrically represented as a unit cone (Figure 2b,c), and can be quantified by the normalized solid angle Ω of such cone (Song, Rohr, et al., 2018):

$$\Omega = \arccos \frac{Q_1 + Q_2}{\sqrt{1+Q_1^2}\sqrt{1+Q_2^2}}. \quad (7)$$

We define $Q_1 = \alpha_{21}/\alpha_{11}$ and $Q_2 = \alpha_{12}/\alpha_{22}$, which represent the extent to which a species depresses the competitor's per capita growth rate relative to its own self-regulation. As shown in Figure 2b,c, the formula to compute the feasibility domain (normalized solid angle) Ω is the same for both coexistence and priority effects—only the slopes are inverted (Appendix S3 for the mathematical derivation). The feasibility domain Ω ranges from 0° to 90° , where $\Omega = 90^\circ$ corresponds to the ecological case where the coexistence of two species is basically impossible and $\Omega = 0^\circ$ corresponds to the case of non-competing species. Thus, the larger Ω , the larger the random changes to the ratio of intrinsic growth rates a community can tolerate without losing coexistence or priority effects.

5 | DISENTANGLING THE ROLES

To disentangle the roles of intrinsic growth rates and competition strengths in shaping coexistence and priority effects, we propose to combine the theoretical tools of MCT and SA. For this purpose, we can rewrite the coexistence criteria (Equation 2) for a two-species LV competition system as

$$\rho < \frac{r_2}{r_1} \sqrt{\frac{Q_2}{Q_1}} < \frac{1}{\rho}. \quad (8)$$

Thus, the niche overlap is now given by $\rho = \sqrt{Q_1 Q_2}$. Note that the fitness ratio ($r_2/r_1 \sqrt{Q_2/Q_1}$) now explicitly expresses the intrinsic growth rates. Table 1 provides the summary of all model parameters and their definition. Following this notation, the necessary and sufficient conditions for coexistence (Equation 2) can be rewritten as $Q_1 < r_2/r_1 < 1/Q_2$, and similarly, for priority effects (Equation 3) they read as $Q_1 > r_2/r_1 > 1/Q_2$. Consequently, the dynamical stability condition for coexistence (i.e. the condition leading to the global stability of a feasible fixed point) is then given by $Q_1 \cdot Q_2 < 1$, while the dynamical instability condition for priority effects is given by $Q_1 \cdot Q_2 > 1$. Note that the exact case $Q_1 \cdot Q_2 = 1$ corresponds to the border between the stability and instability areas.

5.1 | Linking the stabilizing mechanism and SA

Under MCT, the stabilizing mechanism monotonically increases the range of the fitness ratio compatible with species coexistence

(Figure 2a). In other words, the stabilizing mechanism leads to the increase in relative reductions in per capita growth rate compatible with coexistence. It has the opposite effect on priority effects

TABLE 1 Summary of model parameters. The table presents a summary of the main parameters and quantities used across the text

Definition	
Properties	
Feasibility	The existence of an equilibrium point at which all species have a positive abundance
Global stability	The capacity to converge to a unique equilibrium point regardless of the initial abundances
Model parameters	
r_i	Intrinsic growth rate
α_{ij}	Absolute reduction in per capita growth rate (competition strength)
$\bar{\alpha}_{ij} = \alpha_{ij}/r_i$	Relative reduction in per capita growth rate (relative competition strength)
$K_i = r_i/\alpha_{ii}$	Carrying capacity
$Q_i = \alpha_{ij}/\alpha_{ii}$	Reduction in per capita growth rate relative to self-regulation
Important quantities	
r_2/r_1	Ratio of intrinsic growth rates
$\rho = \sqrt{Q_1 Q_2}$	Niche overlap
$\sqrt{\frac{\bar{\alpha}_{11}\bar{\alpha}_{22}}{\bar{\alpha}_{21}\bar{\alpha}_{12}}} = \frac{r_2}{r_1} \sqrt{\frac{Q_2}{Q_1}}$	Fitness ratio
Ω	Feasibility domain (normalized solid angle)

(Figure 2a). However, it is not immediately clear how the stabilizing mechanism affects the tolerance to perturbations in intrinsic growth rates. To link the stabilizing mechanism and SA, we need to ask the two following questions: How does the niche overlap (ρ) relate to the feasibility domain (Ω) when both the fitness ratio ($r_2/r_1 \sqrt{Q_2/Q_1}$) and ratio of intrinsic growth rates (r_2/r_1) are fixed? How does the ratio of intrinsic growth rates (r_2/r_1) affect the feasibility domain (Ω) under the stabilizing mechanism? Note that the ratio r_2/r_1 corresponds to the initial location of a two-species system within the parameter space of intrinsic growth rates. Additionally, recall that the feasibility domain is derived from SA and corresponds to the range of intrinsic growth rates compatible with coexistence or priority effects.

The mathematical link between the stabilizing mechanism of MCT and the angle of SA is provided in Appendix S4. In brief, their combination reveals that the stabilizing mechanism always increases the range of intrinsic growth rates compatible with coexistence (Figure 3). As expected, it has the opposite effect on priority effects (Figure 3). However, the magnitude of these effects depends on the given ratio of intrinsic growth rates (assuming it remains fixed). Specifically, the smaller the niche overlap (ρ), the larger the feasibility domain (Ω) of species coexistence (and the opposite behaviour for priority effects). Yet, the difference in the effect between a small and a large niche overlap (ρ) moves from linear to nonlinear the larger the ratio of intrinsic growth rates (Figure 3). That is, the effect of the stabilizing mechanism on the feasibility domain (Ω) decreases as the ratio of intrinsic growth rates deviates from 1. Moreover, all these effects are stronger under coexistence than under priority effects (Figure 3).

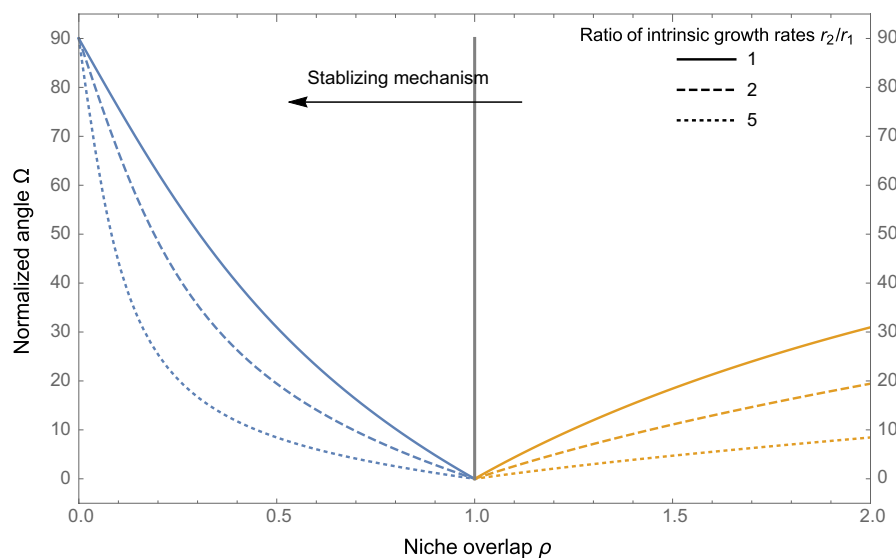


FIGURE 3 Effect of stabilizing mechanism on coexistence and priority effects under perturbations in intrinsic growth rates. Each line corresponds to a different ratio of intrinsic growth rates (r_2/r_1) at fixed fitness ratio ($r_2/r_1 \sqrt{Q_2/Q_1}$). Following each line, we can see that the stabilizing mechanism has a nonlinear positive effect on the feasibility domain Ω for coexistence. The opposite pattern for priority effects. The magnitude of Ω decreases for both coexistence and priority effects the more the ratio of intrinsic growth rates deviates from 1. These effects are stronger under coexistence than under priority effects. For illustration purposes, we use a fitness ratio of 2. Note that all the qualitative results presented here hold for any combination of parameters (Appendix S4). The grey line represents the stability–instability border

This difference is explained by the fact that the stabilizing mechanism operates within a niche overlap between 0 and 1 for coexistence, and within a niche overlap larger than 1 for priority effects. These statements are true for any fitness ratio and given ratio of intrinsic growth rates (Appendix S4). In sum, while explicitly ignored in previous applications of MCT, the ratio of intrinsic growth rates is an important mediator of the extent to which the stabilizing mechanism affects coexistence and priority effects.

5.2 | Linking the equalizing mechanism and SA

Under MCT, the equalizing mechanism centres the fitness ratio within a given range of niche overlap for both coexistence and priority effects (Figure 2a). Note that this is different from the stabilizing mechanism, whose effects on coexistence and priority effects are the opposite. To link the equalizing mechanism and SA, we need to ask the two following questions: (a) How does the fitness ratio ($r_2/r_1\sqrt{Q_2/Q_1}$) need to vary to increase the feasibility domain (Ω) when both the niche overlap (ρ) and ratio of intrinsic growth rates (r_2/r_1) are fixed? (b) How does the ratio of intrinsic growth rates (r_2/r_1) affect Ω under the equalizing mechanism?

The mathematical link between the equalizing mechanism of MCT and the angle of SA is provided in Appendix S4. In brief, the

equalizing mechanism has a non-monotonic effect on the range of intrinsic growth rates compatible with coexistence and priority effects (Figure 4). Specifically, the size of the feasibility domain (Ω) reaches its maximum when the fitness ratio is equal to r_2/r_1 (see horizontal black line in Figure 4), but decreases as the fitness ratio deviates from r_2/r_1 (see curves in Figure 4). Recall that under MCT, the equalizing mechanism maximizes the conditions compatible with coexistence and priority effects when the fitness ratio is equal to 1 (regardless of the value of r_2/r_1), which is known as fitness equivalence (see vertical red line in Figure 4). Thus, as long as $r_2/r_1 \neq 1$, the equalizing mechanism has a non-monotonic effect on the feasibility domain (Ω) under coexistence and priority effects. Moreover, the figure shows that the range of fitness ratio compatible with feasible systems (i.e. $\Omega > 0$) decreases the larger the ratio of intrinsic growth rates (r_2/r_1), revealing a key tolerance trade-off (Appendix S4). Specifically, increasing the tolerance to perturbations in intrinsic growth rates (moving towards increasing Ω) cannot be achieved at the same time as increasing the tolerance to perturbations in competition strengths (moving towards fitness equivalence, viz. equalizing mechanism). This implies that systems may be close to either fitness equivalence (fitness ratio = 1) or a large Ω (fitness ratio = ratio of intrinsic growth rates), but not both. This supports recent work (Song et al., 2019) showing that the equalizing and stabilizing mechanisms are strongly interconnected.

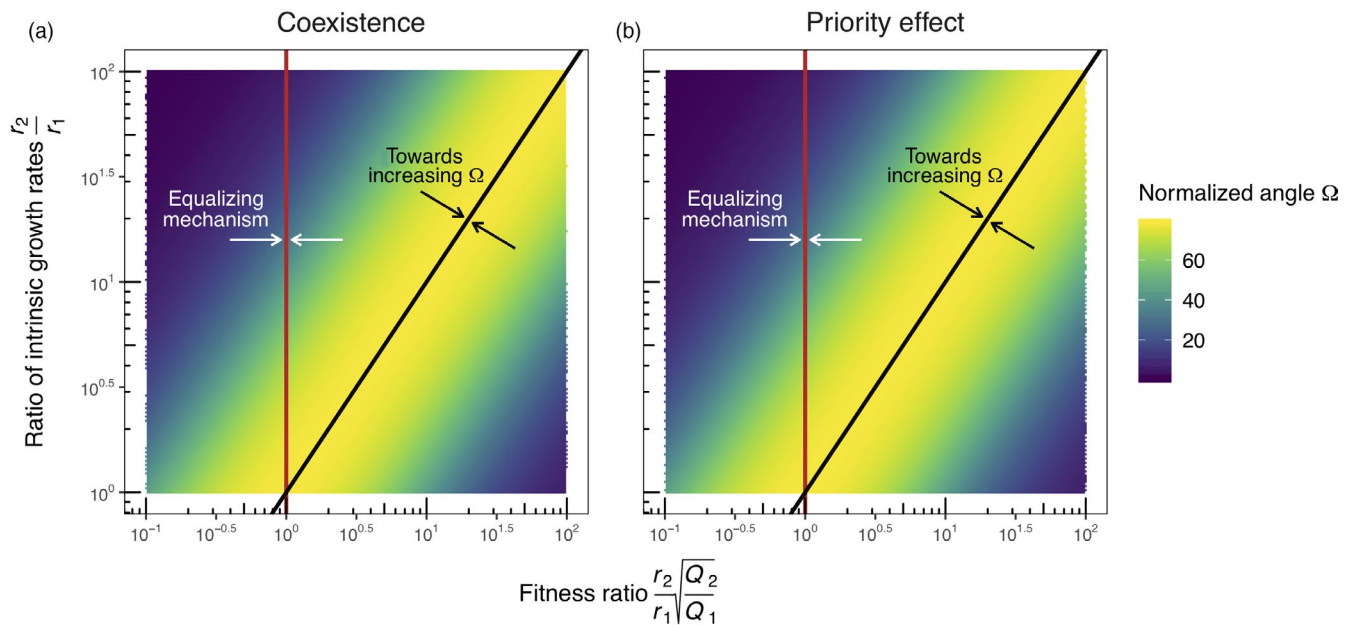


FIGURE 4 Effect of equalizing mechanisms on coexistence and priority effects under perturbations in intrinsic growth rates. Focusing on the tolerance to perturbations in *competition strengths* α_{ij} , it increases following the equalizing mechanism (white arrows), and it is maximized at the fitness equivalence line (red line; see Figure 2 for illustration). Then, focusing on the tolerance to perturbations in *intrinsic growth rates* r_i , it increases following the black arrows, and it is maximized at the one-to-one relationship between fitness ratio and the ratio of intrinsic growth rates (black line). The colours represent the normalized angles Ω of each pair of plant competitors, and the increase in the tolerance to perturbations in intrinsic growth rates can be visualized by the colour gradient. Because the white arrows and the black arrows are generally different, a key trade-off emerges between increasing the tolerance to perturbations in intrinsic growth rates r_i and competition strengths α_{ij} . For illustration purposes, we use $\rho = 0.1$ in (a), and $\rho = 10$ in (b). Note that all the qualitative results presented here hold for any combination of parameters (Appendix S4)

The results above can also be explained intuitively. It is known that the equalizing mechanism counterbalances the ratio of intrinsic growth rates (r_2/r_1) via the ratio of competition strength ($\sqrt{Q_2/Q_1}$). However, under changes in intrinsic growth rates, it is necessary to minimize the niche overlap ($\rho = \sqrt{Q_2 Q_1}$) to increase the likelihood of persistence. Only in the case where $r_2/r_1 = 1$, both the ratio of competition strength ($\sqrt{Q_2/Q_1}$) and niche overlap (ρ) can increase to achieve coexistence (Figure 4). In all the other cases, what it takes to equalize fitness is different from what it takes to find competition strengths that will allow for the greatest range of intrinsic growth rates compatible with coexistence (or priority effects). Hence, the equalizing mechanism imposes a trade-off between the tolerance to perturbations in competition strengths and intrinsic growth rates. Importantly, the magnitude of the trade-off completely depends on the given ratio of intrinsic growth rates (assuming it remains fixed) for both coexistence and priority effects (Figure 4). Note that regardless of the size of the feasibility domain, the starting ratio of intrinsic growth rates determines the amount of random perturbations that can be tolerated. That is, a ratio of intrinsic growth rates in the middle of the feasibility domain can be perturbed in any direction in a magnitude up to half the size of the feasibility domain. Instead, a ratio of intrinsic growth rates close to the border of the feasibility domain can only be perturbed in the opposite direction of that border (see Appendix S5 for illustrative examples). Hence, under arbitrary perturbations, the location of the ratio of intrinsic growth rates shapes the trade-off between tolerance to perturbations in intrinsic growth rates and perturbations in competition strengths.

6 | APPLICATION TO EMPIRICAL DATA

To illustrate how the combination of MCT and SA can allow us to disentangle the effect of perturbations in intrinsic growth rates and competition strengths on coexistence and priority effects, we applied our methods to a dataset of a field system of annual plant competitors occurring on serpentine soils in California, USA (Godoy & Levine, 2014; Kraft et al., 2015). Specifically, the system consisted on the pairwise competition of all possible combinations from 18 annual plant species in experimental gardens by establishing a density gradient of each competitor, and sowing all competitors as focal individuals into that density gradient. The relationships between the fecundity of the focal individuals and the density of a surrounding competitor were fitted to estimate intrinsic growth rates r_i of individual species and pairwise interaction strengths α_{ij} (Godoy & Levine, 2014; Saavedra, Rohr, et al., 2017). A brief summary of the fitting methods and translation to LV parameters is shown in Appendix S6.

We tested two hypothesis derived from our combination of MCT and SA. First, we expected that the effect of niche overlap (ρ) on the range of intrinsic growth rates (Ω) compatible with coexistence should be larger than the range compatible with priority effects

(per Figure 3). Second, if the tolerance to perturbations in intrinsic growth rates is maximized, then we should expect to see their fitness ratio ($\frac{r_2}{r_1} \sqrt{\frac{Q_2}{Q_1}}$) equal to their ratio of intrinsic growth rates ($\frac{r_2}{r_1}$). Instead, if the tolerance to perturbations in competition strengths is maximized, then we should expect to see their fitness ratio ($\frac{r_2}{r_1} \sqrt{\frac{Q_2}{Q_1}}$) equal to one (per Figure 4).

Figure 5 corroborates our hypotheses. Focusing on our first hypothesis, we found that the feasibility domain Ω is typically larger under coexistence than under priority effects (Figure 5a). Under coexistence, Ω increases as the niche overlap decreases, whereas under priority effects we found the opposite pattern. Yet, as expected, the magnitude of such changes was stronger under coexistence than under priority effects. Shifting our focus to our second hypothesis, we found that under both coexistence and priority effects, the tolerance to perturbations in intrinsic growth rates is maximized in the studied empirical systems. Figure 5b,c show that in the majority of the systems, for both coexistence and priority effects, the fitness ratio is close to the ratio of intrinsic growth rates (which corresponds to the 45° line). This observation is statistically confirmed with hypothesis testing (Wilcoxon signed-rank test, $p < 10^{-4}$; Appendix S7). Moreover, in line with our expectations, we observed that the closer the empirical systems are to the one-to-one relationship, the larger the value of Ω they display. Note that these observations are not *circulus in probando* because it is unclear a priori whether the tolerance to perturbations in intrinsic growth rates or in competition strengths would be maximized in these systems. Overall, these results reveal that it is possible to disentangle the effect of external perturbations on empirical systems.

7 | DISCUSSION

Here we have combined the frameworks of MCT and SA to disentangle the effects of perturbations in intrinsic growth rates and competition strengths (absolute reductions in per capita growth rate) on coexistence and priority effects. Under this particular combination of theoretical tools, we have confirmed that the stabilizing mechanism of MCT increases the range of intrinsic growth rates compatible with coexistence, whereas it decreases the range for priority effects. These effects on intrinsic growth rates are stronger under coexistence than under priority effects. Importantly, we have demonstrated that the equalizing mechanism of MCT has a non-monotonic effect on the range of intrinsic growth rates leading to coexistence (or priority effects), and therefore can be used to disentangle the roles of intrinsic growth rates and competition strength. However, the magnitude of all these effects is completely dependent on the given ratio of intrinsic growth rates, introducing a key trade-off between increasing the range of intrinsic growth rates and competition strengths compatible with coexistence or priority effects. That is, the tolerance to different types of perturbations is not maximized at the same time.

Leveraging on the tolerance trade-off found in competing species, the studied empirical data have revealed that the tolerance

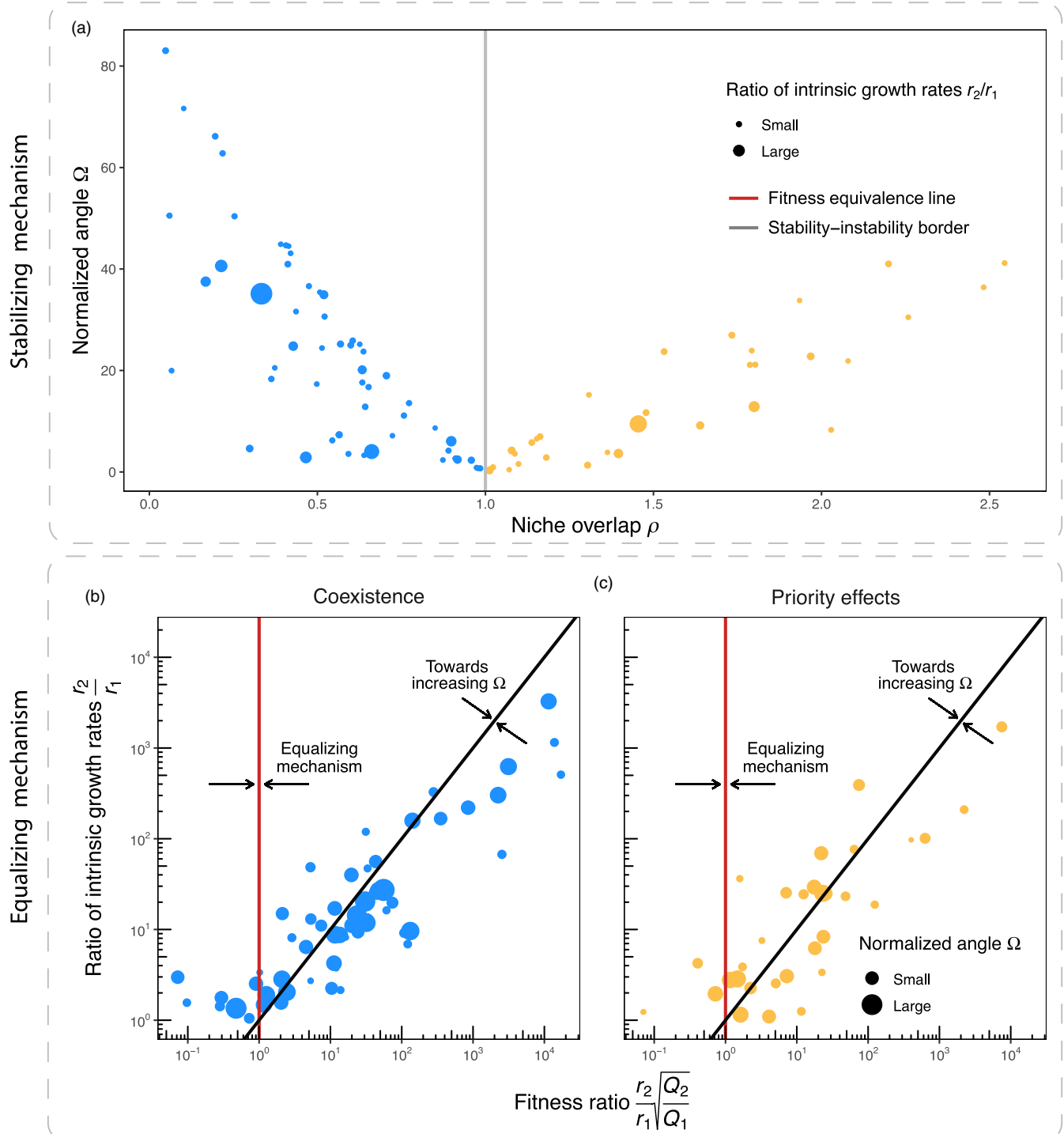


FIGURE 5 Disentangling the role of intrinsic growth rates and competition strengths in annual plant assemblages. The panels illustrate the disentangled contribution of intrinsic growth rates and competition strengths to coexistence and priority effects using parameters estimated from experimental data in annual plant systems (Godoy & Levine, 2014; Kraft et al., 2015). (a) The stabilizing mechanism (niche overlap, ρ) has a stronger effect on Ω under coexistence than under priority effects. The size of the points corresponds to the ratio of intrinsic growth rates (r_2/r_1) for each pair of plant competitors. (b, c) The equalizing mechanism (fitness ratio, $r_2/r_1 \sqrt{Q_2/Q_1}$) exhibits a key trade-off between maximizing tolerance to perturbations in intrinsic growth rates r_i (moving towards increasing Ω) and competition strengths (moving towards fitness equivalence). The black line is the one-to-one relationship between fitness ratio and the ratio of intrinsic growth rates, which theoretically maximizes Ω for a given level of niche overlap (Figure 4). The red line corresponds to the fitness equivalence, which in general maximizes the tolerance to changes in level of competition strengths. The sizes of the points are proportional to the normalized angles Ω of each pair of plant competitors

to perturbations in intrinsic growth rates (not in competition strengths) appears to be maximized in annual plant communities. This result, of course, needs to be taken with caution as some of these experimental systems were not observed in the field. This, however, opens a very exciting opportunity to investigate whether the level of tolerance to perturbations in intrinsic growth rates or competition strengths changes between systems that have been coexisting for shorter or longer periods of time. As another example, one can ask which conditions within the parameter space could allow systems to persist under different habitats, which is an important question in the face of global warming (Alexander, Diez, & Levine, 2015). Similarly, turning the same question upside down, changes in the contributions of different model parameters can be indicative of the direction of perturbations in an environment and the consequent response of species. Because MCT has been widely used for two-competing species under a variety of ecosystems and successional stages (Adler et al., 2013; Bimler et al., 2018; Cardinaux et al., 2018; Chu et al., 2016; Kraft et al., 2015; Levine & HilleRisLambers, 2009; Mordecai et al., 2015; Narwani et al., 2013; Pérez-Ramos et al., 2019), our combined framework can be immediately applied to gain new insights about these questions on empirical systems.

It is also worth mentioning that the most fundamental limitation of our study is that our results apply to two-competing species only. This limitation is given by the canonical formalism of MCT (Barabás et al., 2018; Chesson, 2018; Song et al., 2019). That is, the two-species definitions of niche overlap and fitness ratio in MCT (Equation 5) cannot be generalized to an arbitrary number of competing species. Moreover, the current multispecies definitions in MCT are incompatible with the two-species definitions (Song et al., 2019). Thus, the dynamics of this two-species LV system are simple (necessary and sufficient conditions for coexistence and priority effects have been known for a long time) and special (e.g. dynamical stability is equivalent to invasibility; Goh, 1977). As a consequence, these dynamics do not capture many other components of species coexistence, such as indirect effects (AlAdwani & Saavedra, 2019; Levine et al., 2017; Saavedra, Rohr, et al., 2017) and higher-order interactions (Grilli, Barabás, Michalska-Smith, & Allesina, 2017; Letten & Stouffer, 2019) in multispecies communities. However, we speculate that the tolerance trade-off between intrinsic growth rates and competition strengths may also be present in larger communities.

Overall, our findings illustrate the importance of disentangling the effect of external perturbations on coexistence and priority effects, and calls for further theoretical and empirical investigation about potential tolerance trade-offs shaping different ecological processes (Grainger et al., 2019). For example, Figure 4 shows that communities with the same niche overlap can exhibit exactly the same maximum Ω despite displaying different ratios of intrinsic growth rates (see also Appendix S4). Yet, communities characterized by a large ratio of intrinsic growth rates can exhibit a very different range of conditions compatible with coexistence (and/or priority effects) from communities characterized by a small ratio

(see Appendix S5 for details). Moreover, while we have illustrated the combination of MCT and SA assuming that the ratio of intrinsic growth rates remains fixed, future work can build on our framework to investigate the effect of relaxing this condition on coexistence and priority effects. Similarly, while the tolerance trade-offs that we have found indicate strong constraints between equalizing and stabilizing mechanisms, the formalism followed in this study assumes that either niche overlap or fitness ratio can change while the other remains fixed. Yet, the potential interdependency between these two processes (Song et al., 2019) can make even more stringent the role of different model parameters in the formation of species interactions and dynamics.

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AUTHORS' CONTRIBUTIONS

C.S., R.P.R. and S.S. conceived the ideas and designed the methodology. C.S., R.P.R., D.V. and S.S. analysed data and contributed critically to the draft. C.S. performed the study. S.S. supervised the study. C.S. and S.S. led the writing of the manuscript.

DATA AVAILABILITY STATEMENT

Plant demographic and resource competition data have previously been archived on https://figshare.com/articles/Dataset_Godoy_et_al_2014_Ecology_Letters/4793488 (Godoy, Kraft, & Levine, 2017). The code supporting the results is archived on https://github.com/clsong/JE-Song_et_al-2020 (Song, Rohr, Vasseur, & Saavedra, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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