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A structural approach for understanding multispecies coexistence

Serguei Saavedra[1], Rudolf P. Rohr[2]*, Jordi Bascompte[3],
Oscar Godoy[4], Nathan J. B. Kraft[5], Jonathan M. Levine[6]

sersaa@mit.edu, rudolf.rohr@unifr.ch, jordi.bascompte@ieu.uzh.ch,

ogodoy@irnas.csic.es, nkraft@ucla.edu, jonathan.levine@usys.ethz.ch

[1]Department of Civil and Environmental Engineering, MIT
77 Massachusetts Av., 02139 Cambridge, MA, USA.
[2]Department of Biology - Ecology and Evolution, University of Fribourg
Chemin du Musée 10, CH-1700 Fribourg, Switzerland.
[3]Department of Evolutionary Biology and Environmental Studies, University of Zurich
Winterthurerstrasse 190, CH-8057 Zurich, Switzerland.
[4]Instituto de Recursos Naturales y Agrobiología de Sevilla (IRNAS-CSIC)
Av. Reina Mercedes 10, E-41080 Sevilla, Spain
[5]Department of Ecology and Evolutionary Biology, UCLA
Los Angeles, CA 90095, USA
[6]Institute of Integrative Biology, ETH Zurich
Universitätstrasse 16, CH-8092 Zurich, Switzerland.

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*To whom correspondence should be addressed. E-mail: rudolf.rohr@unifr.ch, Phone: +41 26 300 8851

Abstract

Although observations of species-rich communities have long served as a primary motivation for research on the coexistence of competitors, the majority of our empirical and theoretical understanding comes from two-species systems. How much of the coexistence observed in species rich communities results from indirect effects among competitors that only emerge in diverse systems remains poorly understood. Resolving this issue requires simple, scalable, and intuitive metrics for quantifying the conditions for coexistence in multispecies systems, and how these conditions differ from those expected based solely on pairwise interactions. To achieve these aims, we develop a structural approach for studying the set of parameter values compatible with n-species coexistence given the geometric constraints imposed by the the matrix of competition coefficients. We derive novel mathematical metrics analogous to stabilizing niche differences and fitness differences that measure the range of conditions compatible with multispecies coexistence, incorporating the effects of indirect interactions emerging in diverse systems. We show how our measures can be used to quantify the extent to which the conditions for coexistence in multispecies systems differ from those that allow pairwise coexistence, and apply the method to a field system of annual plants. We conclude by presenting new challenges and empirical opportunities emerging from our structural metrics of multispecies coexistence.

KEYWORDS:
community dynamics, feasibility, invasion criterion, multiple competitors, niche and fitness differences, pairwise effects, structural stability

Introduction

The impressive diversity of species in ecological communities has long motivated ecologists to explore how this diversity is maintained (Darwin, 1859; Hutchinson, 1961). Given that some species are better competitors than others, and that competitive imbalances should lead to the exclusion of inferiors, the factors enabling the coexistence of so many species pose an ecological puzzle. Although observations of species-rich communities have served as a primary motivation for research on coexistence (Hutchinson, 1961; Hubbell, 2001), the majority of our empirical and theoretical understanding of this topic comes from the study of pairwise mechanisms (Case, 2000; Chesson, 2000; Kraft et al., 2015). The reason is one of practicality—experiments and theory devoted to understanding the interaction of two species are simpler and more tractable than efforts to understand the dynamics of many species (Case, 2000). Nonetheless, the focus on pairwise coexistence misses some process that only emerge in diverse systems of competitors and may ultimately maintain coexistence in diverse ecosystems in nature (Billick and Case, 1994).

Theory shows that embedding pairwise competitive interactions into a network of other (still pairwise) competitive interactions causes species to have indirect effects on one another via changes in the abundance of other species in the community (Vandermeer, 1970, 1975; Levine, 1976; Wootton, 1993; Spiesman and Inouye, 2015). These "interaction chains" can reverse pairwise competitive outcomes and strongly affect conditions for coexistence. For example, "rock-paper-scissors" intransitive competition can favor the coexistence of three species, even though each pair cannot coexist in isolation (May and Leonard, 1975; Kerr et al., 2002; Godoy et al., 2017b). With a different set of interactions, conditions for coexistence may be constrained by the more complex network of interactions in diverse communities (May, 1971; Roberts, 1974; Svirezhev and Logofet, 1983; Stone, 1988). Although advancing our understanding of coexistence in systems with

many competitors remains a priority for studies of species diversity maintenance (Logofet, 2005; Edwards and Schreiber, 2010; Allesina and Levine, 2011; Saavedra et al., 2014; Barabás et al., 2016), tools for dissecting how coexistence emerges from population dynamics in higher dimensional systems are only beginning to be developed.

To understand how the structure of diverse competitive networks influences the maintenance of species diversity, ecologists require metrics that both characterize the opportunities for coexistence in n-species systems and quantify how much of this coexistence depends on mechanisms that require more than two species. The approach most commonly applied to understanding coexistence in diverse communities is local stability analysis (May, 1972; Logofet, 1993; Case, 2000). Though related to concepts of stability across the natural sciences, local stability has some central limitations. First, local stability may consider a system stable when not all the constituent species from the community attain positive abundances at equilibrium. This means the system is stable but not feasible (Roberts, 1974; Rohr et al., 2014). Second, the degree to which species coexistence depends on mechanisms that require more than two species cannot be readily calculated from the local stability properties of the n-species equilibrium. Finally and most fundamentally, in local stability analysis the perturbations act on state variables, limiting the analysis to changes in species abundances only. These perturbations may not represent realistic scenarios of changes in species abundances and demographics. Therefore, opportunities for coexistence may be more intuitively and directly evaluated by measuring the robustness of coexistence to both large and small changes in the demographic rates and interactions of the competitors (i.e., the parameters of population dynamics models).

To address these issues above, one can study coexistence from a mutual invasibility perspective, where species' invasion growth rates can be decomposed into stabilizing

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niche differences that increase the conditions for coexistence and average fitness differences that drive competitive exclusion (Chesson, 2000; Adler et al., 2007). Because coexistence requires each of the two competitors to have a positive growth rate when rare, the stabilizing niche difference can be regarded as a metric of the opportunity for coexistence (i.e., how large a fitness difference can be tolerated). Under Modern Coexistence Theory (MCT) (Chesson, 2000), niche differences include all processes that cause intra-specific interactions to be more limiting than interspecific interactions, and thereby benefit species that drop to low relative abundance. Fitness differences include all factors that favor one competitor over the other, and can arise for example from species differences in their innate demographic potential or tolerance of competition (e.g., species differences in their R^* *sensu* Tilman, 1982).

Unfortunately, this two species framework based on invasion growth rates is not easily extended to include mechanisms that only emerge with more than two species. More formally, the invasion criterion can only be used to evaluate n-species coexistence when depressing each species to low abundance allows the remaining n-1 species to coexist (See Appendix S1). Consider, for example, the coexistence of three species via rock-paper-scissors competition. Depressing any one species to low density leads to the elimination of one of the residents. The fact that each species can invade a system with one resident is insufficient to conclude that all three species can coexist (Barabás et al., 2016). Past efforts have extended the two species coexistence framework by quantifying the determinants of population growth rate when invading a system with multiple resident species (Chesson, 2003). This advance has proven useful for understanding how functional trade-offs (Angert, 2009), seed pathogens and predators (Chesson and Kuang, 2010; Stump and Chesson, 2015), and bioclimatic factors (Holt and Chesson, 2014) influence community level metrics of niche differentiation (see also Carroll et al., 2011).

Nonetheless, by building from invasion growth rates and/or averaging over the pairwise niche and fitness differences, these approaches do not readily reveal the contribution of higher dimensional mechanisms to coexistence. In sum, the current set of tools for evaluating species coexistence in diverse communities are not well-suited for differentiating the effects of pairwise mechanisms from those emerging due to the indirect effects among a diverse set of competitors.

In this manuscript, we propose that quantifying the opportunities for coexistence in diverse systems requires moving from mutual invasibility to structural approaches. Recognizing the value of the coexistence metrics developed for two species systems, we develop structural measures analogous to niche differences that quantify opportunities for coexistence in systems of n-competing species. The new measures we propose are based on a structural stability approach previously used to understand the persistence of ecological networks (Rohr et al., 2014; Saavedra et al., 2014, 2016a,b). Developing m tidimensional metrics is important because ecologists ultimately aim to understand the coexistence of many species, not just pairs of competitors. Moreover, the structural metrics we develop allow ecologists to both visualize and quantify the contribution to coexistence of interaction chains that only emerge in systems with more than two species. Though we acknowledge that in species-rich systems each species' per capita effect on another can be modified by the presence of a third species (higher-order interactions- Billick and Case, 1994), this paper will only explore coexistence in competitive systems with species interactions that are fundamentally pairwise. Doing so facilitates quantitative analysis, and also permits the closest connection between our metrics and empirical approaches designed to readily quantify pairwise interactions.

In the first half of the paper, we provide background on the concept and mathematical conditions for species coexistence as achieved through traditional approaches and

compare these to the structural approach developed here. We show how structurally-derived measures map onto the stabilizing niche difference and average fitness difference developed algebraically for systems of two competing species, and then demonstrate how they can be extended to n-species communities. In the second half of the paper, we use our structural measures to develop an approach for quantifying the contribution to coexistence of indirect interactions that only emerge with more than two competitors. We then quantify the contribution of indirect effects to coexistence of three and four species assemblages of annual plant species occurring in California. We conclude by presenting the empirical and theoretical challenges and opportunities emerging from a structural approach.

Species coexistence in simple models

To study species coexistence, first we require a dynamical system describing the change in species abundances through time. The simplest competitive system (but still incorporating the basic elements of a competitive dynamic) for which we have the most analytic results is the Lotka-Volterra model (Volterra, 1931; Lotka, 1932; Case, 2000):

$$dN_i/dt = N_i(r_i - \sum_{j=1}^{n} \alpha_{ij} N_j),$$

where the variable N_i denotes the abundance (or biomass depending on the chosen dimension) of species i; and the parameters $r_i > 0$ and $\alpha_{ij} \geq 0$ represent the intrinsic growth rate of species i and the competitive effect of species j on species i, respectively. Note that the term inside the parenthesis $(r_i - \sum_{j=1}^{S} \alpha_{ij} N_j)$ is called the per-capita growth rate of species i. Importantly, this simple dynamical system can exhibit various complex behaviors: a unique globally stable equilibrium point, multiple locally stable equilibrium, or even limit cycles (Hofbauer and Sigmund, 1998; Case, 2000).

Analyses of the Lotka-Volterra population dynamics model have analytically demonstrated that a necessary condition for species coexistence (see Appendix S2 for further details) is the existence of a feasible equilibrium point (Hofbauer and Sigmund, 1998). An equilibrium point N_i^* is called feasible when the abundance of each species is positive ($N_i^* > 0$). If such a feasible equilibrium point exists, it has to be the solution of the following set of i linear equations (with one equation for each species i):

$$r_i = \sum_{j=1}^{S} \alpha_{ij} N_j^*.$$

These equations make explicit that one needs a particular combination of species demographic parameters (r_i) and interspecific interactions (α_{ij}) to have a positive solution and provide the necessary conditions for species coexistence.

However, feasibility is necessary but not sufficient to guarantee species coexistence in n-species systems. For example, in the textbook case of two competing species (Hofbauer and Sigmund, 1998; Case, 2000), the equilibrium point may be feasible but unstable, and thus one of the competitors will go extinct. While the stability of a feasible equilibrium point is not required for coexistence in higher dimensional systems (Hofbauer and Sigmund, 1998), it has been shown that the global stability of a feasible equilibrium point is a sufficient condition for species coexistence (persistence) (Svirezhev and Logofet, 1983; Logofet, 1993, 2005; Rohr et al., 2014; Saavedra et al., 2016b,a). Therefore, species coexistence can be studied by looking into the necessary conditions for species permanence (that is feasibility) and the necessary and sufficient conditions (that is feasibility and global stability) for species persistence (Hofbauer and Sigmund, 1998; Takeuchi, 1996; Rohr et al., 2014). Unfortunately, in many cases, global stability is very difficult to prove (Logofet, 1993), and one may only rely on the necessary conditions for species coexistence.

Traditional algebraic approach for evaluating 2-species coexistence

To illustrate how species coexistence has traditionally been approached by theory, let us assume that the population dynamics of two competing species can be described by the Lotka-Volterra model, i.e.,

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

Then, if one is interested in the sufficient conditions for coexistence, one needs to find whether there exists a feasible equilibrium point ($N_1^* > 0$, $N_2^* > 0$) and if it is globally stable (see Appendix S3 for a review of global stability).

Traditionally, to find these feasibility and stability conditions, one can draw the non-trivial isoclines, i.e., the two lines defined by $r_1 - \alpha_{11}N_1 - \alpha_{12}N_2 = 0$ and $r - \alpha_{21}N_1 - \alpha_{22}N_2 = 0$ (see Fig. 1A for a graphical example). A feasible equilibrium point exists if the two isoclines cross at a positive abundance, and this equilibrium point is globally stable under the condition $\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$ (Case, 2000). The solution of this dynamical system is given by $N_1^* = \dfrac{\alpha_{22}r_1 - \alpha_{12}r_2}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}$ and $N_2^* = \dfrac{-\alpha_{21}r_1 + \alpha_{11}r_2}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}$. Because the denominator of these two expressions is assumed to be positive, the feasibility conditions can be written as:

$$
\begin{cases}
\alpha_{22}r_1 - \alpha_{12}r_2 > 0 \\
-\alpha_{21}r_1 + \alpha_{11}r_2 > 0
\end{cases}. \tag{2}
$$

These two inequalities can be combined into one equation (given that all parameters are strictly positive):

$$\frac{\alpha_{11}}{\alpha_{21}} > \frac{r_1}{r_2} > \frac{\alpha_{12}}{\alpha_{22}}, \tag{3}$$

which gives the upper and lower bounds within which the relationship of intrinsic growth rates need to fall to allow the feasibility of the system (i.e., a positive solution of the system).

Under the MCT framework (Chesson, 2000), one derives niche and fitness difference metrics from the mutual invasion criterion (rather than the intersecting isocline analysis above, see Appendix S1). Importantly, these metrics for the Lotka Volterra model can also be produced by multiplying each term of Equation (2) by $\sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}}$. This multiplier describes the ratio of species' sensitivities to competition. This results in the inequalities between niche overlap and the fitness difference, given by:

$$\underbrace{\sqrt{\frac{\alpha_{11}\alpha_{22}}{\alpha_{12}\alpha_{21}}}}_{\text{(Niche overlap)}^{-1}} > \underbrace{\frac{r_1}{r_2}\sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}}}_{\text{Fitness difference}} > \underbrace{\sqrt{\frac{\alpha_{12}\alpha_{21}}{\alpha_{11}\alpha_{22}}}}_{\text{Niche overlap}} . \tag{4}$$

By assuming that the niche overlap is less than one, i.e., $\alpha_{12}\alpha_{21} < \alpha_{11}\alpha_{22}$, the global stability of the equilibrium point in a 2-species Lotka-Volterra competition model is guaranteed (Case, 2000).

In this framework, two competing species will coexist if the stabilizing effect of their niche difference (1-Niche overlap) exceeds their average fitness difference (Fig. 2) (Chesson, 1990, 2000, 2012). The greater the stabilizing niche difference (or the smaller the niche overlap), the greater the opportunity for coexistence. Stabilizing niche differences emerge from functional differences between species that cause intra-specific limitation to exceed interspecific limitation, as may arise, for example, from species differences in phenology, habitat specialization, or interactions with specialist consumers (Levine and

HilleRisLambers, 2009; Kraft et al., 2015; Carroll et al., 2011). The average fitness difference is a measure of average competitive ability reflecting species differences in their demographic potential and sensitivity to competition. In the absence of stabilizing niche differences, the species with the higher average fitness excludes the fitness inferior.

A structural approach for species coexistence

As shown in the prior section, the classic algebraic approach for finding the conditions for both feasibility and global stability of a two-competitor system is straightforward. However, this approach becomes difficult if not impossible for n-species (Svirezhev and Logofet, 1983; Logofet, 1993; Takeuchi, 1996; Logofet, 2005). In Box 1, we illustrate how extending this algebraic approach to study the feasibility conditions of more than two species gets into a circularity problem with no solution. Moreover, as noted in the introduction, the mutual invasion criterion—an alternative approach to evaluating coexistence—does not work with more than two species when the depression of one competitor to low density leads to the loss of residents (see Appendix S1). Thus, with traditional approaches, ecologists have limited tools to evaluate the conditions for feasibility and stability in n-species systems. To address this challenge, we suggest to shift from an algebraic to a structural approach (Vandermeer, 1970; Svirezhev and Logofet, 1983; Logofet, 1993). Importantly, this structural approach allows ecologists to evaluate the contribution of indirect effects emerging in multispecies systems to coexistence in diverse communities.

The structural approach involves the study of how the qualitative behavior (e.g., species coexistence as defined by globally stable and feasible solutions) of a dynamical system depends on the parameters of the system itself (Thom, 1972). Nonetheless, as we detail below, this approach parallels developments in coexistence theory aiming to characterize

coexistence as a function of stabilizing niche and fitness differences. Thus, the approach is conceptually aligned with how ecologists have been approaching the problem of the coexistence of two species.

Contrary to the algebraic approach where it is necessary to solve the system of linear equations to derive the inequalities leading to feasibility ($N_1^* > 0$ and $N_2^* > 0$), the structural approach directly evaluates the set of intrinsic growth rates (r_1 and r_2) leading to feasibility given by the geometric constraints imposed through the matrix of competition coefficients $\boldsymbol{\alpha}$. The elements of this matrix correspond to the change in the per capita growth rate of species i under a small change in the density of species j. The matrix $\boldsymbol{\alpha}$ defines then the stability constraints and the range of conditions (parameter values) compatible with feasible solutions (see Appendix S3 for a review about stability conditions). That is, changes in the matrix of competition coefficients correspond to changes in the range of stability and feasibility conditions. This approach has been used to estimate the maximum number of coexisting species (Bastolla et al., 2005, 2009), or how the conditions of feasibility (assuming explicitly global stability) are modulated by species interaction networks (Rohr et al., 2014; Saavedra et al., 2016b,a).

Focusing on the feasibility conditions in the structural approach, given a fixed matrix of competition coefficients ($\boldsymbol{\alpha}$), the set of intrinsic growth rates leading to a feasible equilibrium point is the so-called feasibility domain $D_F(\boldsymbol{\alpha})$. Following a Lotka-Volterra model, this domain can be mathematically written as:

$$D_F(\boldsymbol{\alpha}) = \left\{ \boldsymbol{r} = \begin{bmatrix} r_1 \\ r_2 \end{bmatrix} \in \mathbf{R}^2, \text{ such that } \boldsymbol{\alpha}^{-1}\boldsymbol{r} > 0 \right\}. \tag{5}$$

Note that the expression $\boldsymbol{\alpha}^{-1}\boldsymbol{r} > 0$ corresponds to the condition for an equilibrium point to be feasible (positive solution, $\boldsymbol{N}^* > 0$), that is when the two non-trivial isoclines cross

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at a positive abundance for both species. The elements of the feasibility domain can be written as positive linear combinations of the competitive interaction strengths $\boldsymbol{\alpha}$, i.e,

$$D_F(\boldsymbol{\alpha}) = \left\{ \begin{bmatrix} r_1 \\ r_2 \end{bmatrix} = N_1^* \begin{bmatrix} \alpha_{11} \\ \alpha_{21} \end{bmatrix} + N_2^* \begin{bmatrix} \alpha_{12} \\ \alpha_{22} \end{bmatrix}, \text{ with } N_1^* > 0 \text{ and } N_2^* > 0 \right\}. \qquad (6)$$

Geometrically, the feasibility domain is described by the set of elements between the lines ned by the two column-vectors $\begin{bmatrix} \alpha_{11} \\ \alpha_{21} \end{bmatrix}$ and $\begin{bmatrix} \alpha_{12} \\ \alpha_{22} \end{bmatrix}$. These two lines have a slope of $\alpha\ /\alpha_{11}$ and α_{22}/α_{12}, respectively. Figure 1B provides an illustration of the feasibility domain, and shows that this domain is structurally described by a cone. Note that the inequalities derived under an algebraic approach define the exact same domain. Indeed, a vector of intrinsic growth rates will fall inside the feasibility domain, if and only if its slope given by r_2/r_1 is, respectively, larger and smaller than the slope of the line defining the bottom border of the feasibility cone ($r_2/r_1 > \alpha_{12}/\alpha_{11}$) and the slope of the line defining the top border of the feasibility cone ($r_2/r_1 < \alpha_{22}/\alpha_{12}$), which is equivalent to the inequalities of equation (2).

It is worth noting that the feasibility domain is defined in the same way for any dynamical model for which the feasible equilibrium point can be described by a linear equation, i.e., $\boldsymbol{r} = \boldsymbol{\alpha}\boldsymbol{N^*}$. The Lotka-Volterra model is the classical example of such a model, but a large class of competition models can be described in this way, including models with saturating effects of each additional competitor, the discrete time Lotka-Volterra model, and even the seed banking annual plant competition model.

In the next sections, we illustrate our structural approach with the Lotka-Volterra model. However, in Appendix S4 we summarize models to which our structural framework can be applied; explain how the feasibility domain can be computed; and show how the

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stability constraints of a feasible equilibrium can be studied. Note that for the majority of population models, the strongest condition of stability that one can derive is local asymptotic stability. However, this does not preclude us from applying the structural framework to find the necessary conditions for species coexistence (feasible solutions) in different models. The conditions for stability then remain under the scope and limits of the research question.

onditions for coexistence in a 2-species system

Here we show how one can derive structural measures that parallel algebraic metrics of niche and fitness differences for understanding pairwise coexistence. The structural analog of the niche difference, what we call Ω, corresponds to the normalized solid angle of the cone describing the feasibility domain. This normalization is done such that when the cone of feasibility covers the entire set of positive growth rates (the entire quadrant shown in Fig. 2A), the solid angle equals one ($\Omega = 1$). Note that the absolute magnitude of the growth rates does not change the angle, only the direction. This gives a probabilistic interpretation to the structural analog of the niche difference, i.e., it corresponds to the fraction of positive intrinsic growth rate vectors leading to feasible solutions when sampling uniformly with a fixed norm (e.g., the vector shown in Fig. 2A) (Svirezhev and Logofet, 1983; Logofet, 1993; Saavedra et al., 2016a). The structural analog of the fitness difference, what we called θ, corresponds to the extent to which the vector of intrinsic growth rates ($\boldsymbol{r}$) deviates from the centroid of the domain of feasibility. This deviation is computed by the angle between the centroid of the feasibility domain, what we called $\boldsymbol{r}_c$, and the actually observed vector of intrinsic growth rates. Thus, the centroid of the feasibility domain corresponds on average to the best set of intrinsic growth rate values that can tolerate small random changes without pushing any of the

species to extinction (Rohr et al., 2014; Saavedra et al., 2014; Rohr et al., 2016). Figure 3A shows a graphical representation of the structural analogs of the niche and fitness differences for two species.

thematically, the normalized solid angle (Ω) is computed as follows:

$$\Omega(\boldsymbol{\alpha}) = \frac{2}{\pi} \arcsin\left(\frac{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}}{\sqrt{\alpha_{11}^2 + \alpha_{21}^2}\sqrt{\alpha_{12}^2 + \alpha_{22}^2}} \right), \tag{7}$$

and the centroid of the feasibility domain is defined by the following vector:

$$\boldsymbol{r}_c = \frac{1}{2}\left(\frac{1}{\sqrt{\alpha_{11}^2 + \alpha_{21}^2}} \begin{bmatrix} \alpha_{11} \\ \alpha_{21} \end{bmatrix} + \frac{1}{\sqrt{\alpha_{12}^2 + \alpha_{22}^2}} \begin{bmatrix} \alpha_{12} \\ \alpha_{22} \end{bmatrix} \right). \tag{8}$$

Similarly, analogous to the fitness difference, the deviation (measured in degree) between a given vector of intrinsic growth rates $\boldsymbol{r}$ (i.e., that observed in nature), and that which maximizes the likelihood of a feasible solution $\boldsymbol{r}_c$ is computed based on the scalar product of the two vectors:

$$\theta = \arccos\left(\frac{\boldsymbol{r} \cdot \boldsymbol{r}_c}{\|\boldsymbol{r}\| \cdot \|\boldsymbol{r}_c\|} \right). \tag{9}$$

Therefore, following a structural approach, the feasibility conditions of two-competing species will be fulfilled when the vector defining the intrinsic growth rates of species falls inside the feasibility domain, i.e., when the structural analog of the fitness difference (θ) is small enough relative to the structural analog of the niche difference (Ω). Specifically, these feasibility conditions will be guaranteed as long as $\theta < 45 \cdot \Omega$ (taking θ as degree). Figure 3B illustrates this inequality, which is qualitatively in line with Modern Coexistence Theory's notions (Chesson, 2000) of niche and fitness differences for species coexistence. In general, the figure shows that the higher the structural analog of the niche difference (Ω), the higher the tolerated structural analog of the fitness difference (θ)

leading to feasible solutions. Note that in this 2-species case, the global stability conditions only depend on the matrix of competition coefficients $\boldsymbol{\alpha}$ and are fulfilled when $\alpha \ \alpha_{21} < \alpha_{11}\alpha_{22}$.

tension to multispecies coexistence

The power of the structural approach is that it is readily extended to n-species, and thereby includes and quantifies the contribution to coexistence of the indirect interactions that emerge in systems of three or more competitors. To do so, as in the 2-species case, we need to study the set of intrinsic growth rates compatible with the feasibility of equilibrium points of the system given by a matrix of competition coefficients $\boldsymbol{\alpha}$. The 2-species feasibility domain (Equ. 5) can easily be extended to n-species. As in the 2-species case, we assume that the feasible equilibrium of the dynamical system is the solution of a linear system ($\boldsymbol{r} = \boldsymbol{\alpha}\boldsymbol{N^*}$). This framework can be extended to other population models, such as the seed banking annual plant model (see Appendix S4). The feasibility domain for an n-species community, can be written as

$$D_F(\boldsymbol{\alpha}) = \left\{ \boldsymbol{r} \in \boldsymbol{R}^n_{>0}, \text{ such that } \boldsymbol{\alpha}^{-1}\boldsymbol{r} > 0 \right\}. \tag{10}$$

Writing the elements of the interaction strength matrix $\boldsymbol{\alpha}$ into column vectors, we obtain

$$\boldsymbol{\alpha} = \begin{bmatrix} \alpha_{11} & \cdots & \alpha_{1n} \\ \vdots & \ddots & \vdots \\ \alpha_{n1} & \cdots & \alpha_{nn} \end{bmatrix} = \begin{bmatrix} \vdots & \vdots & & \vdots \\ \boldsymbol{v}_1 & \boldsymbol{v}_2 & \ldots & \boldsymbol{v}_n \\ \vdots & \vdots & & \vdots \end{bmatrix}, \tag{11}$$

and the elements of the feasibility domain are explicitly given by all the positive linear combinations of these column vectors. Thus, the feasibility domain can be rewritten in

the form:

$$D_F(\boldsymbol{\alpha}) = \{\boldsymbol{r} = N_1^* \boldsymbol{v}_1 + N_2^* \boldsymbol{v}_2 + \cdots + N_n^* \boldsymbol{v}_n, \text{ with } N_1^* > 0, N_2^* > 0, \ldots, N_n^* > 0\}. \quad (12)$$

This domain is the conical hull made by the positive combinations of the vectors $\boldsymbol{v}_1$, $\boldsymbol{v}_2$, ..., $\boldsymbol{v}_n$ forming the columns of the matrix of competition coefficients $\boldsymbol{\alpha}$. Geometrically, such a domain is called an algebraic cone. In Figure 4, this algebraic cone is represented by the volume formed by the column vectors of a given matrix of competition coefficients $\boldsymbol{\alpha}$ (green lines). Therefore, the structural analogs of the niche and fitness differences for n-species coexistence can be calculated in a similar fashion as in the 2-species case. The structural analog of the niche difference (Ω) corresponds to the normalized solid angle of the cone describing the feasibility domain. As for two species, the normalization is done such that in the absence of interspecific competition ($\alpha_{ij} = 0$ for all species $i \neq j$) the structural analog of niche difference is equal to one.

The structural analog of the fitness difference (θ) corresponds to the angle between the vector of intrinsic growth rates $\boldsymbol{r}$ and the centroid of the cone defining the feasibility domain ($\boldsymbol{r}_c$). Feasible solutions will be granted as long as the vector of growth rates is inside the cone defining the domain of feasibility. As in the 2-species case, the structural analog of the niche difference Ω in the general n-species case gives the probability of feasible solutions. Note that in n-dimensional systems, the structural analog of fitness difference is inherently a community-level measure, while in MCT it is a pairwise measure even when averaged over multiple invader-resident pairings. See Discussion and Appendix S5 for a detailed comparison between the structural approach and MCT).

The mathematical expressions of these quantities are the following:

$$\Omega(\boldsymbol{\alpha}) = \frac{|\det(\boldsymbol{\alpha})|}{\sqrt[n]{\pi/2}} \int \cdots \int_{\boldsymbol{R}_{\geq 0}^n} e^{-\boldsymbol{x}^T \boldsymbol{\alpha}^T \boldsymbol{\alpha} \boldsymbol{x}} d\boldsymbol{x}. \tag{13}$$

$$\boldsymbol{r}_c = \frac{1}{n} \left(\frac{\boldsymbol{v}_1}{\|\boldsymbol{v}_1\|} + \frac{\boldsymbol{v}_2}{\|\boldsymbol{v}_2\|} + \cdots + \frac{\boldsymbol{v}_n}{\|\boldsymbol{v}_n\|} \right) \tag{14}$$

$$\theta = \arccos \left(\frac{\boldsymbol{r} \cdot \boldsymbol{r}_c}{\|\boldsymbol{r}\| \cdot \|\boldsymbol{r}_c\|} \right) \tag{15}$$

The mathematical derivation, as well as the numerical evaluation, of the structural analog of niche difference Ω are provided in Appendix S6. Note that Svirezhev and Logofet (1983) have already developed a similar formula to compute the normalized solid angle of the feasibility domain for competition systems (see also Saavedra et al. (2016a)). Their formula estimated the proportion of the feasibility domain intersecting the unit simplex, and can be interpreted as a normalized solid angle in what is called the topology L . Note that a unit simplex is the generalization of a triangle with unit area to n-dimensions. The R-code for computing the structural niche and fitness difference is provided on Dryad (Saavedra et al., 2017)

It is worth recalling that the feasibility condition, in and of itself, is a necessary but insufficient condition for persistence or permanence and therefore coexistence (see Appendix S2). Assuming the feasibility conditions are satisfied, the global stability of the feasible equilibrium point is a sufficient condition of coexistence. In dimension 2 the global stability condition is trivial (Case, 2000), but it may become very difficult in dimension n. These types of conditions have been intensively investigated for linear and non-linear Lotka-Volterra models (Svirezhev and Logofet, 1983; Logofet, 1993; Takeuchi, 1996; Logofet, 2005). We summarized these stability conditions in Appendix S3 and then we explain how they can be applied to several population dynamical models in Appendix

S4.

As mentioned above, the feasibility domain is geometrically represented by a cone. To simplify this geometric representation, we can draw one of its sections by projecting it on the unit simplex (Svirezhev and Logofet, 1983; Logofet, 1993). For instance, in the 2-species case this projection is given by a line (Fig. 5A). The gray line represents the full domain of the parameter space of intrinsic growth rates, but normalized such that their sum is equal to one (projection on the unit simplex). Each ending of the gray line represents the case where only one species has an intrinsic growth rate of 1. In turn, the green line represents the projection of the cone defining the feasibility domain on the unit simplex. The two green dots and the orange dot correspond to the two green lines and the orange line of Figure 3A, respectively. Therefore, they define the borders and the centroid of the feasibility domain on the geometric projection, respectively.

This geometric projection on the unit simplex can be, in a similar way, extended to n-species. Figures 5B and 5C provide an illustration for the case of 3 and 4 species. In the case of 3 species, the unit simplex is represented by the gray triangle and the feasibility domain is represented by the inner green triangle. For 4 species, the unit simplex is represented by a pyramid (gray) with triangular faces, and the feasibility domain by an inner green pyramid. In these two cases, as in the 2-species case, the green dots represent the extreme borders of the feasibility domain, and the orange dot corresponds to the centroid. The R-code for reproducing the figures is provided on Dryad (Saavedra et al., 2017)

Disentangling the sources of coexistence

As mentioned in the introduction, one of longest-standing questions in community ecology concerns the importance for coexistence of indirect interactions that emerge when pairwise interactions are embedded into a network of competitors (Yodzis, 1988; Wootton, 1993; Billick and Case, 1994). A central challenge has been differentiating the effects of pairwise interactions from those emerging from the indirect effects generated in the population dynamics of multispecies systems. While the indirect effects of competitors, as emerge in rock-paper-scissors competitive dynamics, have been studied under a game theoretical approach (Kerr et al., 2002; Allesina and Levine, 2011) and partly determine the stability properties of the community matrix (Case, 1990), it has remained unclear how to embed these population dynamics into metrics that show their influence on the potential for coexistence, such as the stabilizing niche difference.

Our basic approach for evaluating the contribution of interaction chains to coexistence (i..e, how much of the conditions for community coexistence is due to indirect competitive effects versus pairwise niche differences) involves two steps. First, the structural approach is used to calculate the feasibility domain of a community, what we denoted by D_F. Note that this feasibility domain is the region of intrinsic growth rates compatible with the coexistence of n species as defined by the matrix of competition coefficients. Second, the structural approach is used to identify the region of intrinsic growth rates compatible with the coexistence of each pair of species, what we denote by D . In turn, the intersection of all the pairwise feasibility domains corresponds to the region of intrinsic growth rates compatible with the coexistence of all pairs, what we denote by $D_{all} = D_{12} \cap D_{1n} \cap \ldots \cap D_{m1} \cap \ldots \cap D_{mn}$, but not necessarily the same as the simultaneous coexistence of all competitors D_F.

We illustrate this approach for the coexistence of three species based on an arbitrary and globally stable three-species competition system given by the positive definite matrix $\boldsymbol{\alpha} = \left[\begin{smallmatrix} 1 & 0.4 & 0.3 \\ 0.5 & 1 & 0.6 \\ 0.05 & 0.5 & 1 \end{smallmatrix} \right]$ in Fig. 6. The feasibility domain for the pair formed by species 1 and 2 (D_2) is represented by the green inner triangle (Fig. 6A). This feasibility domain corresponds to the set of vectors of growth rates over which species 1 and 2 will coexist assuming species 3 is absent. Away from the bottom axis of the simplex, species 3 has positive growth and is therefore present in the system. However, in these projections of purely pairwise coexistence, the ratio of the growth rates of species 1 and 2 compatible with their coexistence is independent of the effects of species 3. Hence, with increasingly greater growth of species 3 (moving upward in Fig. 6A), a green triangle is drawn that retains the ratio of species 1 and 2's growth rates compatible with their coexistence. This pairwise feasibility domain can then be illustrated for all three species pairs, as in Fig. 6B. The intersection of the three green inner triangles (the darkest green area) gives the domain of coexistence for all pairs (D_{all}), i.e., each pair of species can coexist in the absence of the third species. Importantly however, and consistent with predictions from algebraic approaches (e.g., Case, 1990), the intersection of the three pairwise feasibility domains does not properly predict the conditions for 3-species coexistence (see Fig. 6C). The different set of growth rates compatible with the coexistence of all pairs (D_{all}) versus the coexistence of the triplet (D_F) is visualized by overlaying the two feasibility domains (see Fig. 6D).

Our example (Fig. 6D) identifies three regions of community dynamics with a different match between pairwise coexistence (D_{all}) and the full community coexistence (D_F): (i) All pairs show coexistence as does the triplet (the region of overlap, $D_{all} \cap D_F \neq \emptyset$). (ii) All pairs show coexistence but not the triplet (the region of D_{all} not overlapping with D). (iii) Not all pairs show coexistence but the triplet does (the region of D_F not

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overlapping with D_{all}). Importantly, these cases illustrate the varying effects that indirect effects among competitors can have on coexistence. These indirect effects can create conditions for coexistence that do not otherwise occur with purely pairwise mechanisms (as in iii), they can constrain coexistence (as in ii), or they can have no effect on the qualitative outcome of competition (as in i).

The example in Fig. 6, where the feasibility domain for the full community (D_F) is only partially the same as that predicted by the intersection of pairwise coexistence (D_{all}) proves to be just one of three general cases. The first general case is that in which the n-species feasibility domain may lie entirely within the feasibility domain predicted by the coexistence of all pairs (Figure 7A), as occurs with the globally stable matrix defined by interaction coefficients $\boldsymbol{\alpha} = \begin{bmatrix} 1 & 0.4 & 0.5 \\ 0.5 & 1 & 0.6 \\ 0.4 & 0.5 & 1 \end{bmatrix}$. In this case, the indirect interactions emerging in the three-species system contract the conditions for coexistence relative to that predicted by pairwise mechanisms alone. For instance, if the set of intrinsic growth rates is located anywhere inside the dark region (e.g., orange point), species in all the three pairs and the triplet will coexist.

The second general case is that shown in Figure 7B (the same network is shown in Fig. 6), where there is partial overlap between the feasibility domain of the entire community and that of pairwise coexistence. Importantly, even though the two feasibility domains are of roughly comparable area, the indirect interactions in this case cause three species coexistence to require different competitor growth rates than the coexistence of all pairs. For instance, if the set of intrinsic growth rates is located at the orange point (inside the region of overlap), the species in all the pairs and the triplet will coexist. However, if the set of intrinsic growth rates is located at the red point (outside the region of overlap), then we can observe triplet coexistence but not the coexistence of the pair formed by species 2 and 3.

The third general case is that in which there is no overlap between the feasibility domain of the entire community and that of pairwise coexistence. This is exemplified by Figure 7C, where the interaction coefficients $\boldsymbol{\alpha} = \begin{bmatrix} 1 & 1.5 & 0.1 \\ 0.1 & 1 & 0.6 \\ 1.6 & 0.5 & 1 \end{bmatrix}$ produce a rock-paper-scissors competitive loop. In this example, the feasibility domains for all three pairs do not overlap and thus there exists no set of growth rates that allow all pairs to coexist ($D_{ll} = \emptyset$). If one chooses a vector of intrinsic growth rates in the middle of the darker region (red point), species 3 outcompetes species 2 in absence of species 1 (the point is outside of the pair-wise region described by the left side of the outer triangle, and closer to species 3), species 1 outcompetes species 3 in absence of species 2 (the point is outside of the pair-wise region described by the right side of the outer triangle, and closer to species 1), and species 2 outcompetes species 1 in absence of species 3 (the point is outside of the pair-wise region described by the bottom side of the outer triangle, and closer to species 2). Nonetheless, the feasibility domain for the full three-species systems is not empty, indicating that the indirect interactions caused by the rock-paper-scissors competitive structure increase the opportunity for coexistence.

To quantify the contribution to coexistence of indirect interactions only emerging with more than two competitors, one can calculate a pair of related metrics. The first metric, what we call community-pair differential (Δ), quantifies the degree to which coexistence is more or less easily obtained with the inclusion of indirect effects only emerging with more than two species. Specifically, one can calculate the difference in the size of the feasibility domain for the full n-species community versus that allowing the coexistence of all pairs. Mathematically, this is given by $\Delta = \Omega - \Omega_{all}$, where Ω is the structural analog of niche difference and Ω_{all} is the fraction of intrinsic demographics compatible with the coexistence of all pairs in the community. We calculated Ω_{all} using a simple Monte Carlo approach by randomly sampling vectors of intrinsic growth rates uniformly on the sphere

(R-code provided on Dryad (Saavedra et al., 2017)). Note that this metric can only take values between $[-1, 1]$. A positive value indicates greater opportunities for coexistence in the full community (as in Figure 7C), a negative value indicates less opportunities for coexistence (as in Figure 7A). In other words, a positive value of community-pair differential indicates that indirect interactions promote more opportunities of coexistence as it would be expected from the intersection of pairwise niche differences, and vice versa for negative values.

The community-pair differential, however, tells us nothing about the degree to which the pairwise mechanisms actually explain the coexistence of all n species, i.e., the degree to which the two feasibility domains overlap. Thus, the second metric, what we call community-pair overlap (ω), involves calculating the proportion of the feasibility domain for the entire community (D_F) that lies inside the feasibility domain under which all pairs coexist (D_{all}). We calculated ω following the same Monte Carlo approach used for the previous metric (Code in R provided as Supplemental Material). This metric can only take values between $[0, 1]$. The smaller the value, the more the coexistence of the n-species requires demographic rates different than those allowing pairwise coexistence. In other words, the smaller the value the stronger the importance of indirect interactions for species coexistence. For instance, a value of one would indicate complete overlap as in the case shown in Figure 7A, whereas a value of zero would indicate no overlap as in the case of Figure 7C.

In sum, these two metrics evaluate whether the coexistence of all n-species is more easily obtained than the equivalent coexistence for all pairs of n species (Δ), and the degree to which the conditions for pairwise coexistence are the same as those required for the coexistence of all species in the community (ω). Of course, the alternative arrangements of the feasibility domains can be visually inspected in the three species simplex. However,

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for systems with more than three species, where the feasibility domains cannot be directly examined, these metrics are essential for evaluating the effects of indirect interactions. Note that this approach can be applied to any competition matrix regardless of its stability properties (with its corresponding dynamical interpretation). Both the community-pair differential and the community-pair overlap describe regions of the feasibility domain, which correspond to the necessary conditions for species coexistence.

Quantifying the sources of coexistence in a field system

To illustrate how the structural approach can quantify the extent to which indirect effects influence coexistence in nature, we applied our methods to a field system of annual plant competitors occurring on serpentine soils. In prior work (Godoy et al., 2014; Kraft et al., 2015), we have quantified the pairwise interactions between 18 annual plant species in experimental gardens established in the field in California. We did so by establishing a density gradient of each competitor, and sowing all competitors as focal individuals into that density gradient. We then fit relationships between the fecundity of the focal individuals and the density of a surrounding competitor to estimate each pairwise interaction coefficient. In addition, we quantified all key demographic rates for the 18 species (germination, survival of ungerminated seeds, and innate fecundity), which in combination with the fitted interaction coefficients (α), can be used to parameterize a standard model of competing annual plants with a seed bank (see Appendix S4). Data are provided on figshare (Godoy et al., 2017a).

Using the fitted pairwise interactions, we formed all possible communities of three and four species of the 18 species, and filtered (giving 27% and 6% of the total number of

triplets and quadruplets) those that generated D-stable matrices. Note that D-stable matrices are those that are locally stable for any feasible equilibrium point (see Appendix S3). Recall that conditions for global stability with this annual plant model in n-dimensional systems are not known (Case, 2000). Importantly, our results were qualitatively the same without filtering. We then calculated the metrics of community-pair differential (Δ) and community-pair overlap (ω) for all D-stable triplets and quadruplets. Thus, results correspond to the necessary conditions for species coexistence and D-stable systems.

As an illustration of the empirical cases, Figure 8 shows the feasibility domains (projected onto a unit simplex) of two different triplets and one quadruplet formed with the empirically measured pairwise interactions. These feasibility domains can be located anywhere within the unit space of species demographic values, and can overlap (Panel A) or not overlap (Panel B) the feasibility domain allowing for the coexistence of all pairs within the triplet. In fact, we found that in only 11 out of 138 stable triplets (7%) the feasibility domain of the community D_F lies completely inside the intersection of all pairwise feasibility domains D_{all}. In 80% of cases D_F lies partially inside D_{all}, and in the other 13% of cases D_F is completely different from D_{all}. For empirically-constructed quadruplets, we found that in 51 out of 81 (63%) cases D_F lies partially inside D_{all}, and in the remaining 37% of cases D_F has no overlap with D_{all}. Thus, these qualitative analyses indicate that indirect effects among competitors frequently change the demographic rates required for coexistence. To provide a quantitative analysis of these effects, we can apply the community-pair differential and community-pair overlap measures to all these communities.

We find that the feasibility domain for the triplets and quadruplets is most frequently of comparable size to the domain allowing the coexistence of all pairs ($\Delta \approx 0$) (Figure 9A).

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In some cases the opportunity for coexistence is less than that for all pairs of species, and in modestly more cases, the opportunity for coexistence is greater. This suggests that indirect effects have no systematic effect on the conditions for coexistence in triplets and quadruplets of the studied annual plant species. A related question is how much of the opportunity for coexistence in the three or four-species assemblages rests on indirect effects, i.e., demographic rates different than those allowing the coexistence of all pairs.

Figure 9B shows that although in the majority of cases the feasibility domains of the triplets and quadruplets overlap with the domains that allow all pairs to coexist ($w > 0$), only in about 15 percent of triplets and less than 5 percent of quadruplets this overlap is more than 0.9. In fact, the most likely community-pair overlap is near zero ($\omega \approx 0$) indicating that demographic rates allowing the coexistence of all three species in the triplets and quadruplets are completely different than those allowing the coexistence of all pairs within the communities. In these cases, coexistence at least partly depends on indirect effects among the competitors as the reduction of the system to a series of isolated pairs would not give the coexistence of all species.

Overall, these results reveal that in this annual plant community, indirect effects emerging with more than two species can help stabilize coexistence, but these effects are almost equally likely to harm coexistence, and in most cases, have modest effects. Moreover, as one may anticipate, pairwise interactions become less reliable indicators of species coexistence with increasing species richness.

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derstanding the processes enabling the coexistence of three or more competitors has long proven challenging because the outcome of their interaction depends on the

combined effects of pairwise coexistence mechanisms and those emerging from the indirect interactions that only emerge in multispecies systems (Levine, 1976; Stone, 1988). A major hurdle to understanding has been the dearth of metrics that can be used to characterize opportunities for coexistence in multispecies systems. We believe that the structural approach developed here better positions ecologists to overcome these challenges.

The proposed structural measures of multispecies coexistence are directly derived from the population dynamics of the n-competing species, as can be described by a range of continuous and discrete time models (see Appendix S4). Different from an algebraic approach, the structural approach allows one to compare the coexistence predicted by simple pairwise interactions to that predicted when those interactions are embedded in a network of other interactions. With these metrics, ecologists parameterizing models of competition can evaluate the extent to which observed coexistence rests on the indirect interactions that emerge when species are embedded in competitive networks. It is important to recall that these metrics allow us to understand the necessary (feasibility) conditions for species coexistence. Sufficient conditions (e.g., global stability) are very difficult to derive for n-dimensional systems in some population dynamics models (Hofbauer and Sigmund, 1998; Logofet, 1993), but they can certainly be investigated in future research.

We would also like to stress that the approach to quantifying pairwise niche differences and average fitness differences under MCT (Chesson, 2000) and the structural approach presented here are similar to one another but not the same. The similarity lies in the fact that coexistence requires the (structural) fitness differences to lie within the bounds set by the (structural) niche difference. However, the fitness difference defined under MCT includes species differences in their innate demographic potential discounted by their

general sensitivity to competition (with details varying by model), as this determines the competitive dominant in the absence of any stabilizing niche difference. By contrast, in the structural approach, species differences in their sensitivity to competition shift the feasibility domain and can affect its width. Moreover, in contrast to the 2-species case, multispecies coexistence cannot be predicted with structural analogs of the niche and fitness differences only. This arises because feasibility domains of the same extent can differ in their geometry (see Appendix S7), implying that communities with the same likelihood of coexistence may be robust to different directions of environmental disturbances (changes to the demographic rates).

Unfortunately the limitation above for multispecies systems is not easily solved, but one possible solution involves computing the asymmetry of the feasibility domain to study how different drivers can change regions of coexistence. This asymmetry can be estimated by the variation among all the n-faces of the given multidimensional cone, and computed by the variance of all the n-structural analog of niche differences generated after independently removing each of the n-species from the community (see Appendix S7). This measure of asymmetry may lead to a better understanding of the dynamical relationship between a community's tolerance to perturbation and changing pairwise interactions. We acknowledge that ideally the MCT and structural approaches would perfectly match, but the structural approach we develop here has the advantage of being scalable to multispecies communities, and we encourage future work to find better analogs between the MCT and structural approaches.

Importantly, our structural approach gives empirical ecologists new tools to explore the controls over coexistence in networks of pairwise interactions. Prior approaches show how one can quantify the impact of species on one another via chains of indirect interactions (Wootton, 1993; Yodzis, 1988), and classic theory can be used to evaluate how the

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addition or removal of species from communities influences local stability of the multispecies equilibrium (May, 1972; Roberts, 1974). But these methods do not easily reveal the contribution to coexistence of indirect effects that only emerge in multispecies systems, as can be understood from the structural stability metrics developed here.

Of course, using these metrics requires that empiricists parameterize models of competition with field data, a task that can be quite labor intensive in diverse systems. Nonetheless, an increasing number of studies parameterize competition models with information on the demographic performance of focal individuals, and their response to variation in competitor density and identity (e.g., Godoy et al., 2014; Chu and Adler, 2015). These parameterization should be constrained to the spatial scale under investigation. With the structural metrics developed here, one can then evaluate a range of problems about multispecies coexistence in field settings. First, the structural analog of niche difference reveals the likelihood of coexistence given different innate growth rates for the competing species. This metric can therefore be compared across communities in different experimental contexts to evaluate how different factors contribute to the robustness of coexistence. For example, one can ask how climate warming modifies opportunities for coexistence in systems of three or more competitors, and whether its effects on diversity result from changes to the interaction coefficients or species' innate growth rates. Second, by quantifying how robust coexistence is to variation in the growth rates of competitors, ecologists can evaluate the variation among species pairs in the strength of their niche differences. One can ask, for example, how evenly distributed is niche differentiation among the members of a community, revealing whether the persistence of some species is more robust to changing growth rates than others.

Finally, and as demonstrated here for assemblages of annual plant species, one can evaluate how chains of interactions among competitors contribute to, or detract from,

multispecies coexistence. As illustrated in Figures 6-9, this contribution or detraction can be measured by predicting the growth rates compatible with the coexistence of all species pairs (in isolation from the rest of the community), and comparing this region to the growth rates compatible with the coexistence of all species embedded in the full matrix of interaction coefficients. Based on the analysis of the annual plant system presented here, we anticipate that many communities should exhibit regions of separation between n-species and pairwise coexistence, indicating a significant contribution of indirect effects to possible coexistence. Further empirical measures of interaction coefficients in other systems are of course needed to properly test the generality of these predictions. More generally, our field annual plant example illustrates that the structural approach can be applied with competition models quite different than Lotka Volterra, and that it can be fully parameterized with field data.

Looking ahead, we see several interesting theoretical directions following from the work developed here. As we have shown, one challenge that arises from mechanisms of coexistence emerging in n-dimensional systems is that the coexistence of the entire community in no way guarantees that sub-units of that community are also feasible and stable (Fig. 7). This raises the interesting question of how such communities assemble from less diverse systems (consider assembling a community with rock-paper-scissors competition one species at a time). Fortunately, our metrics and approach could also be useful for understanding the most likely order of assembly and disassembly in ecological communities. Each change in the composition of a community brings together a change in the feasibility domain, widening or shrinking the conditions compatible with the coexistence of all residents with a new species. In fact, previous work has shown that during the assembly and disassembly of ecological communities, feasibility is either maximized or preserved through time (Saavedra et al., 2016a,b), suggesting that the

order of assembly and disassembly might be anticipated based on the feasibility properties of the community.

A second promising opportunity to build on the approach developed here involves the inclusion of higher-order interactions that emerge in species-rich competitive systems. The insights gained from our metrics rest on the assumption that the interactions between species are fundamentally pairwise. A more holistic view of indirect interactions in diverse competitive communities acknowledges that species can affect one another by altering the abundance of shared competitors, but also by modifying the per capita effect of one species on another (Wootton, 1993; Billick and Case, 1994). Ecologists have limited understanding of the importance of these higher-order interactions, in part because quantifying their importance in field systems with many competitors is exceedingly difficult. Thus, while our approach focused on pairwise interactions is a useful and realistic first step for empirical studies (Vandermeer, 1969), future theory exploring how and whether higher-order interactions in multispecies systems influence coexistence would be an important next step.

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Author contributions SS and RPR performed the study and contributed equally to the work. SS, RPR, JB, and JML contributed to the design of the study; OG, NJBK and JML provided the empirical data; SS, RPR, and JML wrote the first draft of the manuscript; all authors contributed to revisions.

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Box 1: Algebraic approaches to feasibility cannot be extended to more than two species.

One might attempt to extend the two species isocline approach to evaluate feasible equilibria in systems of n-competing species. However, the inequalities derived for two species do not exist for three or more species. That is, first one would have to solve the linear equations defining the feasible equilibrium point:

$$\begin{cases} N_1^* = \frac{1}{\det(\boldsymbol{\alpha})} \left((\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32})r_1 + (\alpha_{13}\alpha_{32} - \alpha_{33}\alpha_{12})r_2 + (\alpha_{12}\alpha_{23} - \alpha_{22}\alpha_{13})r_3\right) \\ N_2^* = \frac{1}{\det(\boldsymbol{\alpha})} \left((\alpha_{23}\alpha_{31} - \alpha_{33}\alpha_{21})r_1 + (\alpha_{11}\alpha_{33} - \alpha_{13}\alpha_{31})r_2 + (\alpha_{13}\alpha_{21} - \alpha_{23}\alpha_{11})r_3\right) \\ N_3^* = \frac{1}{\det(\boldsymbol{\alpha})} \left((\alpha_{21}\alpha_{32} - \alpha_{31}\alpha_{22})r_1 + (\alpha_{12}\alpha_{31} - \alpha_{32}\alpha_{11})r_2 + (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})r_3\right) \end{cases},$$

which is basically the inverse of the matrix $\boldsymbol{\alpha}$ multiplied by the vector of intrinsic growth rates $\boldsymbol{r}$. Then the feasibility constraints would result in the following three inequalities:

$$\begin{cases} (\alpha_{22}\alpha_{33} - \alpha_{23}\alpha_{32})r_1 + (\alpha_{13}\alpha_{32} - \alpha_{33}\alpha_{12})r_2 + (\alpha_{12}\alpha_{23} - \alpha_{22}\alpha_{13})r_3 > 0 \\ (\alpha_{23}\alpha_{31} - \alpha_{33}\alpha_{21})r_1 + (\alpha_{11}\alpha_{33} - \alpha_{13}\alpha_{31})r_2 + (\alpha_{13}\alpha_{21} - \alpha_{23}\alpha_{11})r_3 > 0 \\ (\alpha_{21}\alpha_{32} - \alpha_{31}\alpha_{22})r_1 + (\alpha_{12}\alpha_{31} - \alpha_{32}\alpha_{11})r_2 + (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})r_3 > 0 \end{cases}.$$

These inequalities would have to assume that $\det(\boldsymbol{\alpha}) > 0$, which is a necessary condition for global stability. At the point at which one would try to combine these inequalities, we would enter into a circularity problem without any way to solve it. For example, let us take the two first inequalities and let us derive and upper and lower bound between which the ratio r_1/r_2 has to fall to provide a positive solution to the system. Inevitably, these upper and lower bounds will be a function of the intrinsic growth rate of the third species (r_3). The same schema repeats with species 2 and 3, and with species 3 and 1, in a circular way. Therefore, we cannot derive simple inequalities defining the feasibility of n-species, such as those given in two-species systems.

Figure 1: **Algebraic and structural representation of two species coexistence.** Panel **A** shows the classic algebraic approach of assessing whether two competing species coexist by looking at the non-trivial isoclines. Panel **B** depicts the structure or parameter space (feasibility domain) leading to species coexistence, given a matrix of competition coefficients. The feasibility domain is given by the area between the two green lines, and it is defined by the range of intrinsic growth rates under which the two isoclines cross at positive abundances (in Panel **A**). To ensure coexistence (provided that the stability condition is satisfied, see Appendix S2), the intrinsic growth rates (represented by the brown vectors) have to fall inside the two green lines.

Figure 2: **Modern coexistence theory for 2-species coexistence.** This figure illustrates how the niche and fitness difference define the domain of coexistence of pairs of species. It is derived from Equation 4 and assuming, without loss of generality, that $r > r_2$.

Figure 3: **Structural analogs of the niche and fitness differences defining 2-species coexistence.** Panel **A** shows the structural analogs of the niche difference (Ω) and fitness difference (θ) for an arbitrary matrix of competition coefficients $\boldsymbol{\alpha}$ fulfilling global stability conditions (see Appendix S3). The green lines define the border of the feasibility domain. The normalized solid angle Ω between these two green lines corresponds to the structural analog of the niche difference. The brown vector ($\boldsymbol{r}$) corresponds to a given set of intrinsic growth rates, the dashed orange line corresponds to the centroid of the cone ($\boldsymbol{r}_c$), and the angle (measured in degree) between the centroid and the vector of intrinsic growth rates corresponds to the structural analog of the fitness difference. Panel **B** corresponds to the analysis of 2-species coexistence following the structural approach. The bottom green region corresponds to the area of coexistence.

Figure 4: **Illustration of the structural approach for multispecies coexistence.** For an arbitrary positive-definite matrix of competition coefficients $\boldsymbol{\alpha}$ with 3 competing species, the figure illustrates the structural analogs of the niche Ω and fitness differences θ. The coordinates in the figure correspond to the parameter space of intrinsic growth rates. The structural analog of the niche difference is the solid angle (Ω) of algebraic cone of feasibility, under which the community can sustain stable and feasible solutions. This cone is delimited by the column vectors of the matrix of competition coefficients $\boldsymbol{\alpha}$. The structural analog of the fitness difference corresponds to the angle (θ) between any observed vector of intrinsic growth rates $\boldsymbol{r}$ (brown solid vector) and the centroid of the feasibility domain $\boldsymbol{r}_c$ (dashed line).

Figure 5: **Geometric projection of the cone defining the feasibility domain.** For arbitrary, positive-definite, interaction strength matrices $\boldsymbol{\alpha}$, Panels **A-C** illustrate the geometric projection of the feasibility domain on the unit simplex for 2, 3, and 4 species, respectively. These projections give an easier geometric representation of the feasibility domain. The unit simplex is defined by the set of all positive intrinsic growth rates that sum to one. In each panel, each of the extremes on the line corresponds to the case where one species has an intrinsic growth rate of 1 and the others have an intrinsic growth rate of zero. In the middle of each line, the two corresponding species have the same intrinsic growth rate of 0.5. In the 2-species case, this geometric projection corresponds to a line, in the 3-species case corresponds to a triangle, and in the case of 4-species corresponds to a pyramid.

Figure 6: **Community versus pairwise effects on coexistence.** Panel **A** depicts the feasibility domain of the pair formed by species 1 and 2 (D_{12}). If one chooses a vector of intrinsic growth rates inside the green triangle, then in absence of species 3, species 1 and 2 will coexist. Panel **B** shows the three domains of feasibility for each pair of species (D_{ij}). Note that if one chooses a vector of intrinsic growth rates at the intersection of these three domains, then any pair of species will coexist in the absence of the third species (D_{all}). Panel **C** shows the domain of feasibility of the three species together (D_F). Panel D shows the overlap between the domain of feasibility of the triplet (D_F) with the pairwise domains (D_{ll}). This is depicted by scenario (i). It can also be seen that pairwise coexistence does not automatically imply triplet coexistence (ii), and vice versa (iii).The difference between these two domains is indicative of the importance of indirect interactions for multispecies coexistence.

Figure 7: **Three general cases of community and pairwise coexistence.** Panel **A** shows an example where the feasibility domain of the triplet (D_F) is completely inside the pairwise coexistence domain (D_{all}). If the vector of intrinsic growth rates is located at the orange dot, each pair coexists in isolation and the three species can coexist. Panel **B** shows the case where pairwise (D_{all}) and community coexistence (D_F) do not fully overlap. The orange dot corresponds to the scenario describe in Panel **A**, whereas the red dot corresponds to a scenario where the triplet coexists, but not species 2 and 3 in isolation. Panel **C** corresponds to a rock-paper-scissors case. This figure shows a community in which the feasibility domain of the three pairs do not intersect ($D_{all} = \emptyset$). If we choose the vector of intrinsic growth rate at the red dot, we obtain a rock-paper-scissors dynamic, i.e, each species is out-competed by another species in absence of the third.

Figure 8: **Illustration of feasibility domains for triplets and quadruplets of annual plant species in a California field system.** Panels **A** and **B** show the feasibility domains for two triplets, and Panel **C** for a quadruplet based on the empirically measured interaction coefficients (Godoy et al., 2014; Kraft et al., 2015). These feasibility domains are all projected on a unit simplex as shown for artificially-constructed interaction matrices in Figures 5-7. Here, the demographic rates compatible with coexistence correspond to the seeds produced per seed lost from the system as explained in Appendix S4. The four letter species codes correspond to *Agoseris heterophylla* (AGHE), *Centaurea melitensis* (CEME), *Hemizonia congesta* (HECO), *Lasthenia californica* (LACA), *Lotus wrangeliensis* (LOWR), Clarkia purpurea (CLPU), *Navarretia atractyloides* (NAAT), and *Geranium carolinianum* (GECA).

Figure 9: **Quantifying the sources of multispecies coexistence in annual plant assemblages.** For fitted competition coefficients obtained in an annual plant system (Godoy et al., 2014; Kraft et al., 2015), panels **A** and **B** show the community-pair differential (Δ) and the community-pair overlap (ω), respectively. The community-pair differential evaluates whether the coexistence of all n-species is more easily obtained than all pairs of n species. Positive values indicate that the feasibility domain for the community (D_F) is larger than the feasibility domain of pairwise coexistence (D_{all}). The community-pair overlap evaluates the degree to which the conditions for pairwise coexistence are the same as those required for the coexistence of all the species in the community. The smaller the value, the more the feasibility domain of the community differs from the feasibility domain allowing pairwise coexistence.
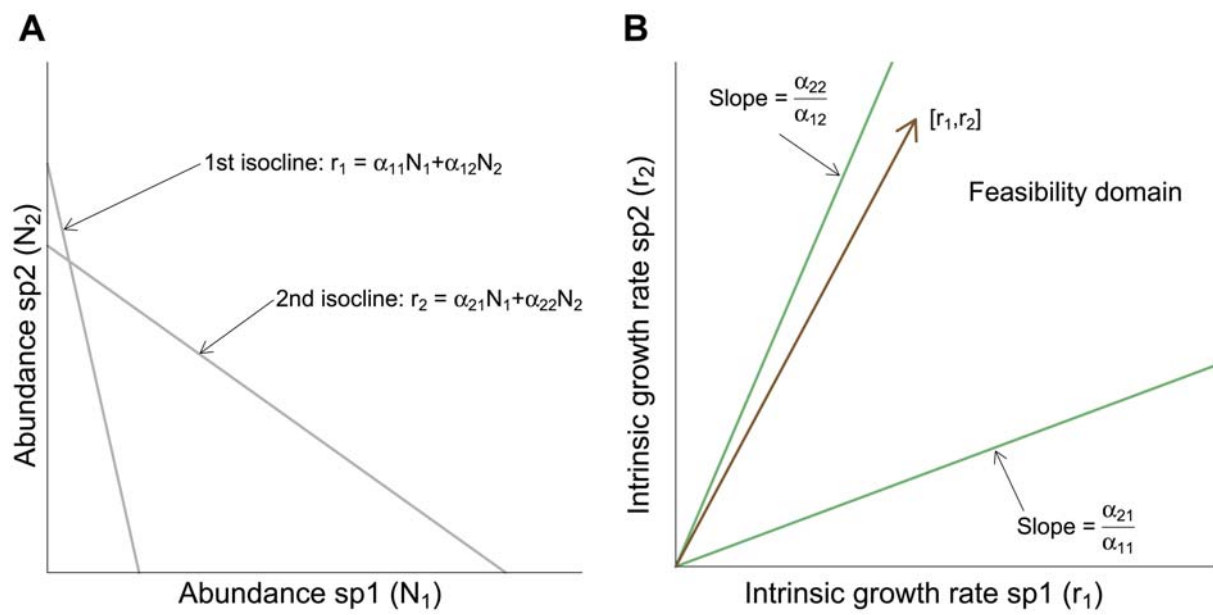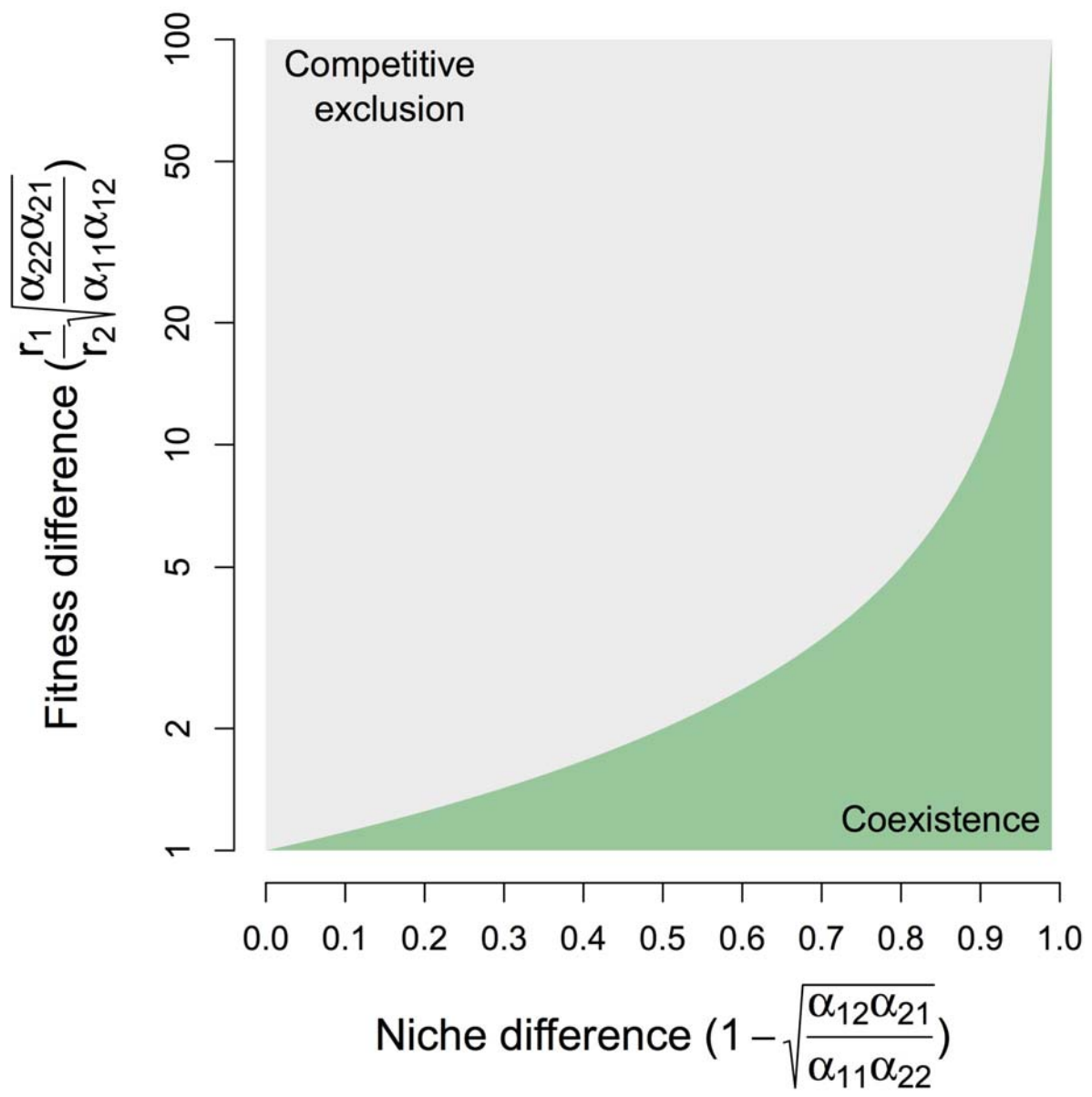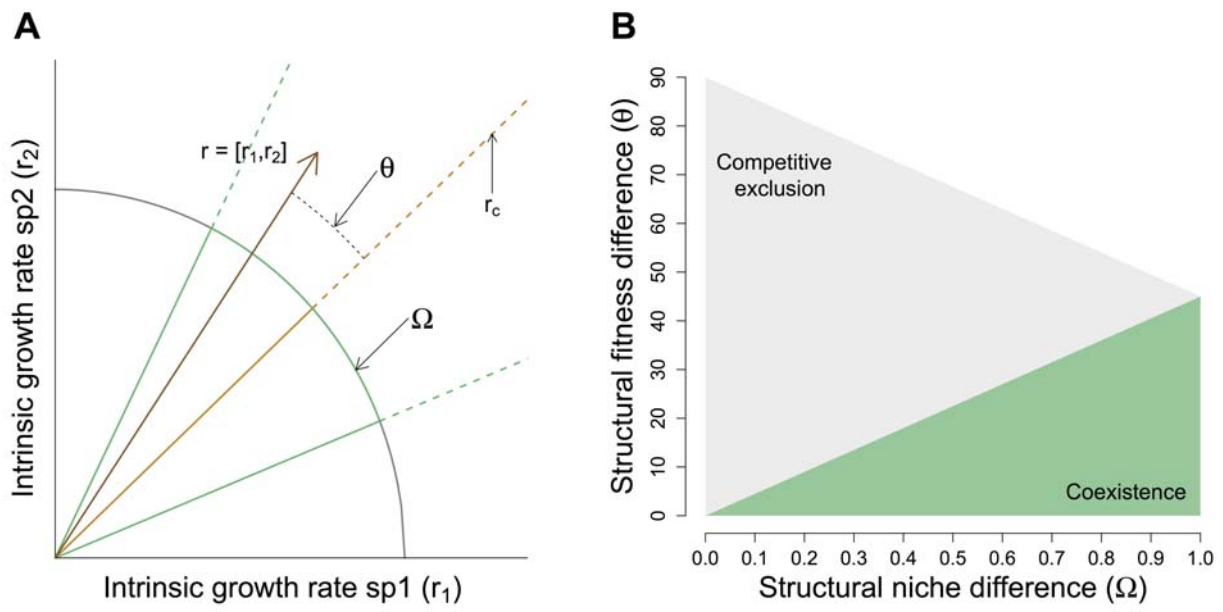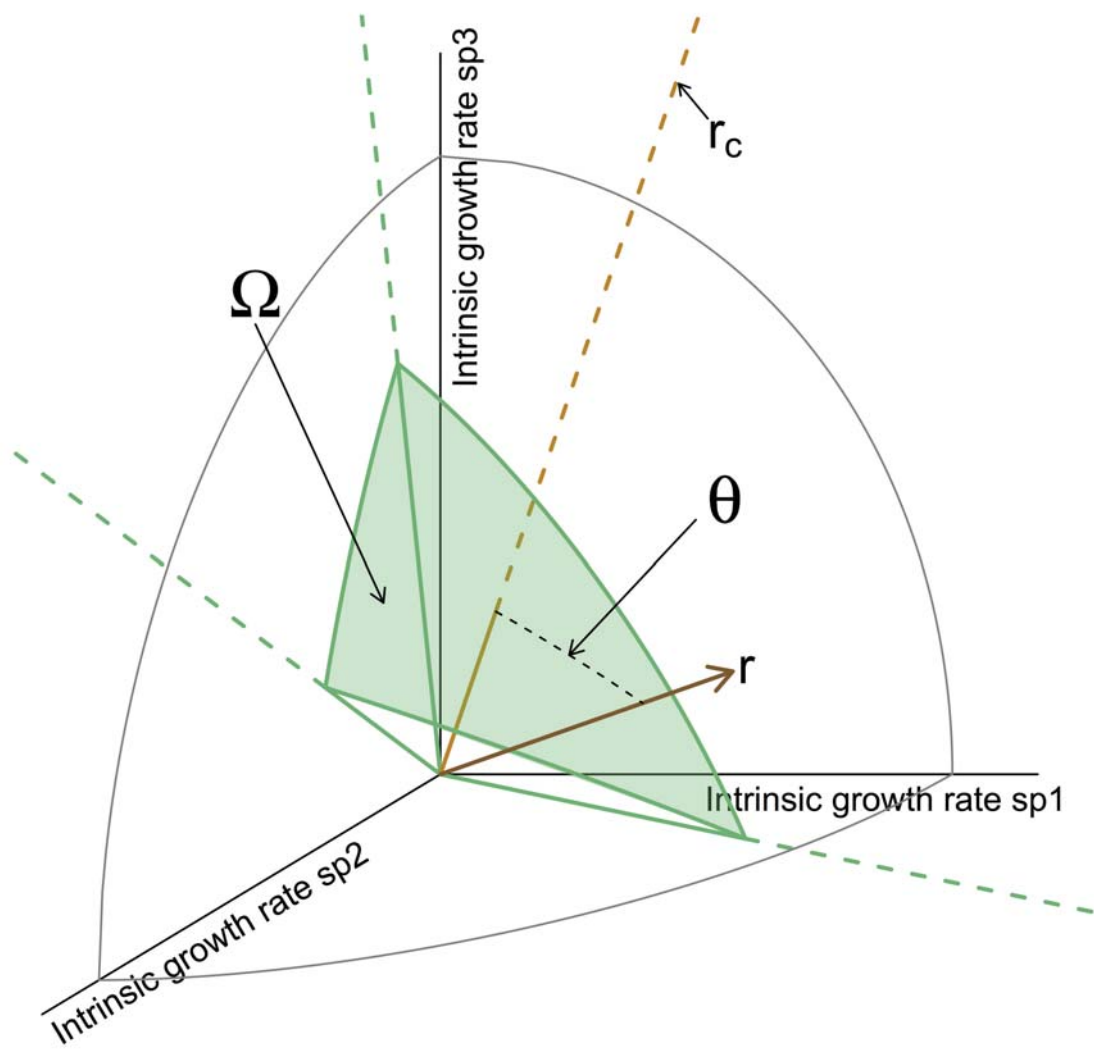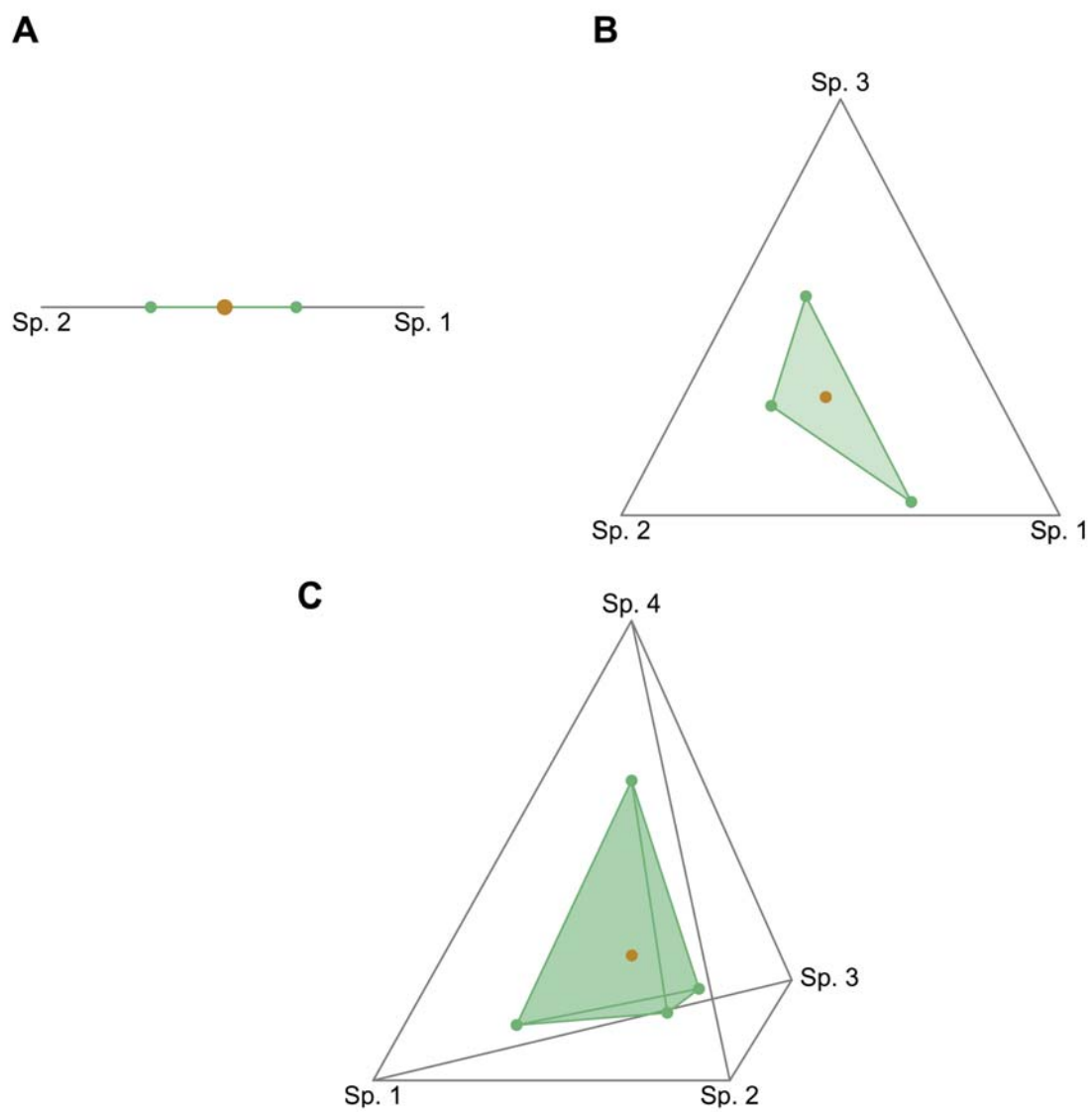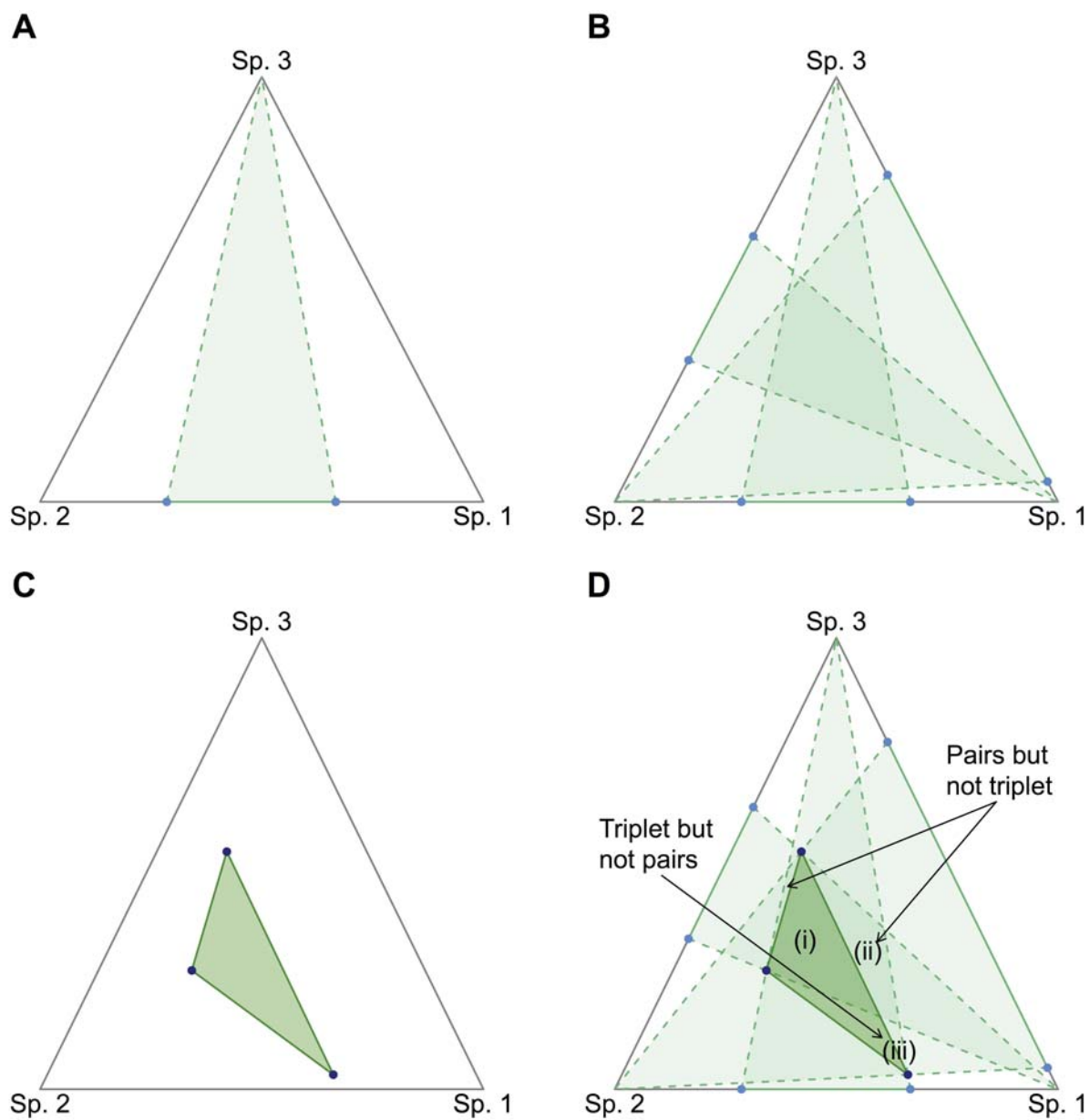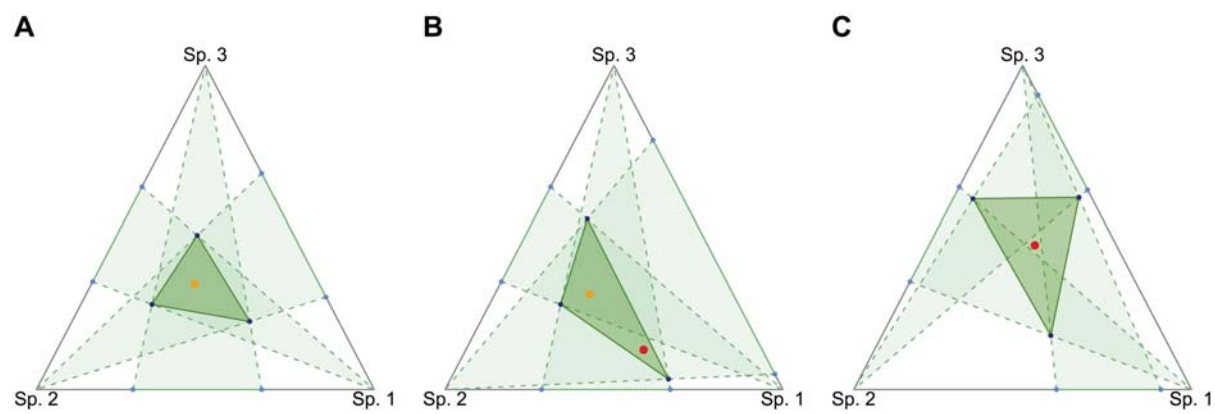
Figure1.

Figure2.

Figure3.

Figure4.

A

B

C

Figure5.

Figure6.

Figure 7.

Figure8.

Figure9.