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A structural approach for understanding multispecies coexistence

Serguei Saavedra,[1] Rudolf P. Rohr,[2,7] Jordi Bascompte,[3] Oscar Godoy,[4]
Nathan J. B. Kraft,[5] and Jonathan M. Levine[6]

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

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 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.

Key words: 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. 2017*b*). 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,

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[7] Corresponding Author. E-mail: rudolf.rohr@unifr.ch

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 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, 2016*a, b*). Developing multidimensional 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)

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

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 $\alpha_{ij} \geqslant 0$ 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 $\left(r_i - \sum_{j=1}^{S} \alpha_{ij} N_j\right)$ 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. 2016*a, b*). 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 (Takeuchi 1996, Hofbauer and Sigmund 1998, 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 Two-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.,

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

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 $r_2 - \alpha_{21}N_1 - \alpha_{22}N_2 = 0$ (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 $N_1^* = (\alpha_{22}r_1 - \alpha_{12}r_2)/(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})$ and $N_2^* = (-\alpha_{21}r_1 + \alpha_{11}r_2)/(\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})$. 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)

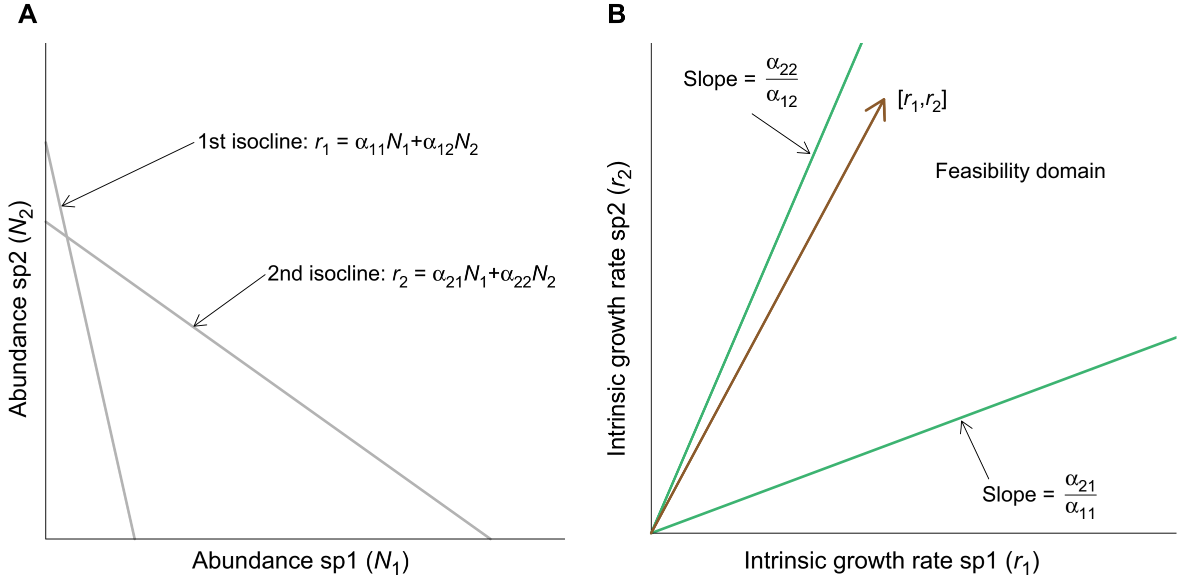

FIG. 1. Algebraic and structural representation of two-species coexistence. Panel A shows the classic algebraic approach of assessing whether two competing species coexist by looking at the non-trivial isoclines. Panel B depicts the structure or parameter space (feasibility domain) leading to species 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 S3), the intrinsic growth rates (represented by the brown vectors) have to fall inside the two green lines. [Color figure can be viewed at wileyonlinelibrary.com]

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

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 Eq. 2 by $\sqrt{\alpha_{22}\alpha_{21}/\alpha_{11}\alpha_{12}}$. 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 two-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, Carroll et al. 2011, Kraft et al. 2015). 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, 2005, Takeuchi 1996). 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

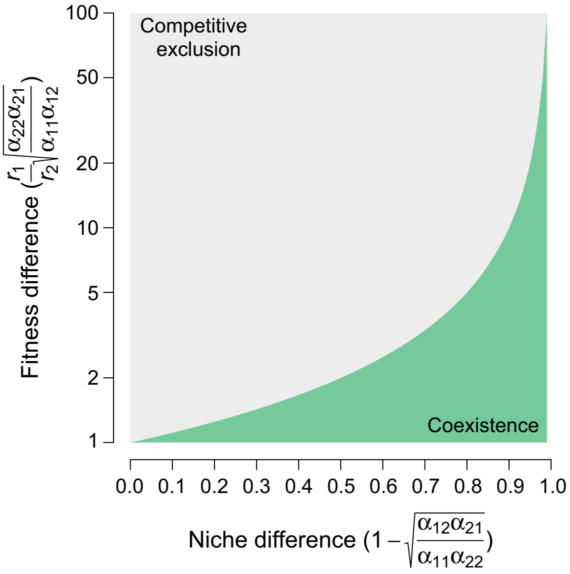

FIG. 2. Modern coexistence theory for two-species coexistence. This figure illustrates how the niche and fitness difference define the domain of coexistence of pairs of species. It is derived from Eq. 4 and assuming, without loss of generality, that $r_1 > r_2$. [Color figure can be viewed at wileyonlinelibrary.com]

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

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

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

which is basically the inverse of the matrix $\boldsymbol{\alpha}$ multiplied by the vector of intrinsic growth rates $\mathbf{r}$. 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.

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. 2016*a, b*).

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

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

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

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

Geometrically, the feasibility domain is described by the set of elements between the lines defined by the two column-vectors $[\alpha_{11} \quad \alpha_{21}]$ and $[\alpha_{12} \quad \alpha_{22}]$. These two lines have a slope of α_{21}/α_{11} and α_{22}/α_{12}, respectively. Fig. 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 Eq. 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., $\mathbf{r} = \boldsymbol{\alpha}\mathbf{N}^*$. 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 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.

CONDITIONS FOR COEXISTENCE IN A TWO-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. 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. 2016*a*). The structural analog of the fitness difference, what we called θ, corresponds to the extent to which the vector of intrinsic growth rates ($\mathbf{r}$) 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 $\mathbf{r}_c$, 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, 2016, Saavedra et al. 2014). Fig. 3A shows a graphical representation of the structural analogs of the niche and fitness differences for two species.

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

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

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

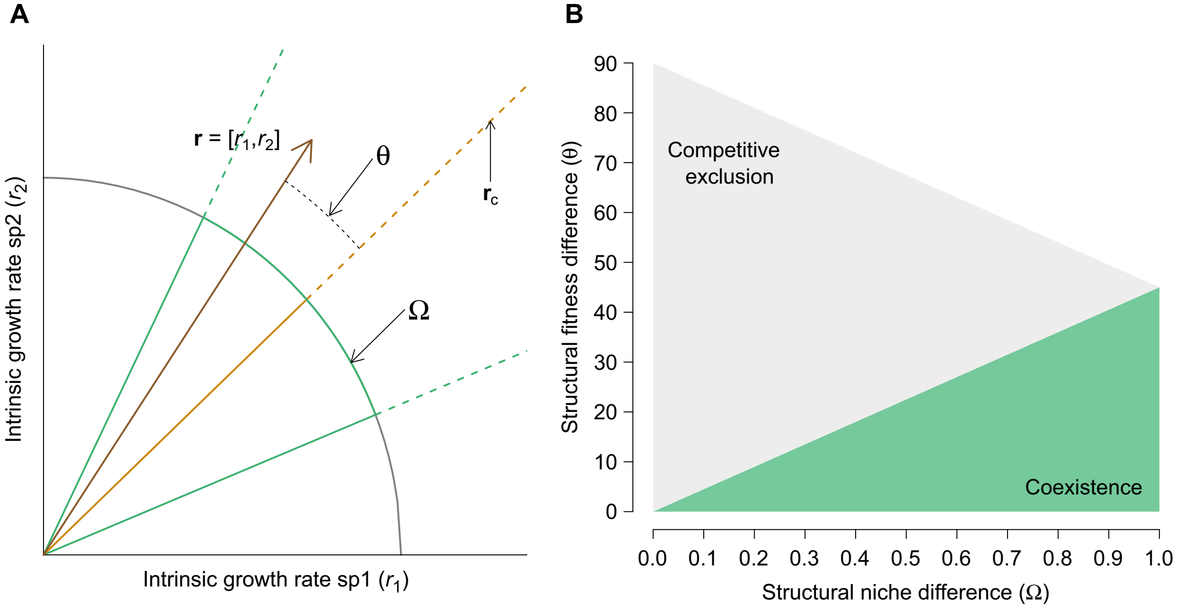

FIG. 3. Structural analogs of the niche and fitness differences defining two-species coexistence. Panel A shows the structural analogs of the niche difference (Ω) and fitness difference (θ) for an arbitrary matrix of competition coefficients $\boldsymbol{\alpha}$ fulfilling global stability conditions (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 (**r**) corresponds to a given set of intrinsic growth rates, the dashed orange line corresponds to the centroid of the cone ($\mathbf{r}_c$), 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 two-species coexistence following the structural approach. The bottom green region corresponds to the area of coexistence. [Color figure can be viewed at wileyonlinelibrary.com]

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

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

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

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). Fig. 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 two-species case, the global stability conditions only depend on the matrix of competition coefficients $\boldsymbol{\alpha}$ and are fulfilled when $\alpha_{12}\alpha_{21} < \alpha_{11}\alpha_{22}$.

EXTENSION 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 two-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 two-species deasibility domain (Eq. 5) can easily be extended to n-species. As in the two-species case, we assume that the feasible equilibrium of the dynamical system is the solution of a linear system ($\mathbf{r} = \boldsymbol{\alpha}\mathbf{N}^*$). 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

$$D_{\mathrm{F}}(\boldsymbol{\alpha}) = \left\{ \mathbf{r} \in \mathbf{R}^{n}_{>0}, \text{ such that } \boldsymbol{\alpha}^{-1}\mathbf{r} > 0 \right\}. \tag{10}$$

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

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

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

$$\begin{aligned} D_{\mathrm{F}}(\boldsymbol{\alpha}) = \{ \mathbf{r} = N_1^*\mathbf{v}_1 + N_2^*\mathbf{v}_2 + \cdots + N_n^*\mathbf{v}_n, \\ \text{with } N_1^* > 0, N_2^* > 0, , N_n^* > 0 \}. \end{aligned} \tag{12}$$

This domain is the conical hull made by the positive combinations of the vectors $\mathbf{v}_1, \mathbf{v}_2, \ldots, \mathbf{v}_n$ forming the columns of the matrix of competition coefficients $\boldsymbol{\alpha}$. Geometrically, such a domain is called an algebraic cone. In Fig. 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 two-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.

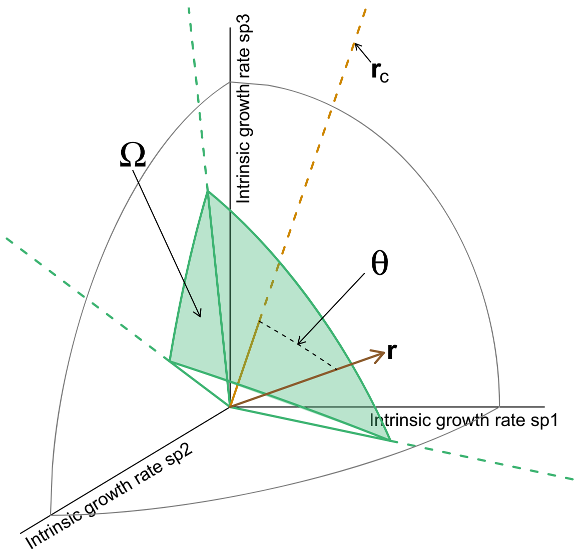

FIG. 4. Illustration of the structural approach for multi-species coexistence. For an arbitrary positive-definite matrix of competition coefficients $\boldsymbol{\alpha}$ with three competing species, the figure illustrates the structural analogs of the niche Ω and fitness differences θ. The coordinates 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 $\mathbf{r}$ (brown solid vector) and the centroid of the feasibility domain $\mathbf{r}_c$ (dashed line). [Color figure can be viewed at wileyonlinelibrary.com]

The structural analog of the fitness difference (θ) corresponds to the angle between the vector of intrinsic growth rates $\mathbf{r}$ and the centroid of the cone defining the feasibility domain ($\mathbf{r}_{\mathrm{c}}$). 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 two-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:

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

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

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

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. 2016*a*). 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_1. 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, 2005, Takeuchi 1996). 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 two-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 Fig. 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. Fig. 5B and C provide an illustration for the case of three and four species. In the case of three species, the unit simplex is represented by the gray triangle and the feasibility domain is represented by the inner green triangle. For four 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 two-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 vs. 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_{ij}. In turn, the intersection of all the

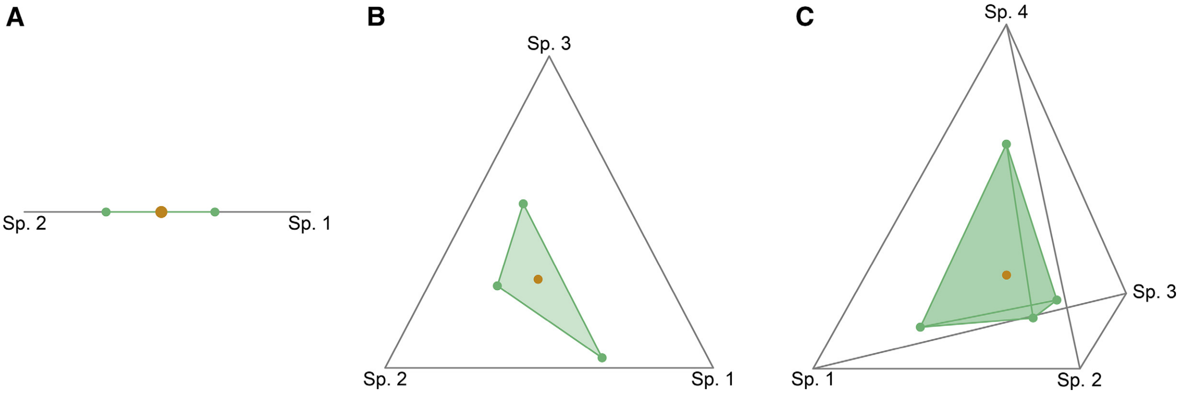

FIG. 5. Geometric projection of the cone defining the feasibility domain. For arbitrary, positive-definite, interaction strength matrices $\boldsymbol{\alpha}$, Panels A–C illustrate the geometric projection of the feasibility domain on the unit simplex for two, three, and four species, respectively. 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 two-species case, this geometric projection corresponds to a line, in the three-species case corresponds to a triangle, and in the four-species case corresponds to a pyramid. [Color figure can be viewed at wileyonlinelibrary.com]

pairwise feasibility domains corresponds to the region of intrinsic growth rates compatible with the coexistence of all pairs, what we denote by $D_{\text{all}} = D_{12} \cap D_{13} \cap \ldots \cap D_{1S} \cap \ldots \cap D_{S-1,S}$, 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

$$\boldsymbol{\alpha} = \begin{bmatrix} 1 & 0.4 & 0.3 \\ 0.5 & 1 & 0.6 \\ 0.05 & 0.5 & 1 \end{bmatrix} \text{ in Fig. 6.}$$

The feasibility domain for the pair formed by species 1 and 2 (D_{12}) 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 three-species coexistence (see Fig. 6C). The different set of growth rates compatible with the

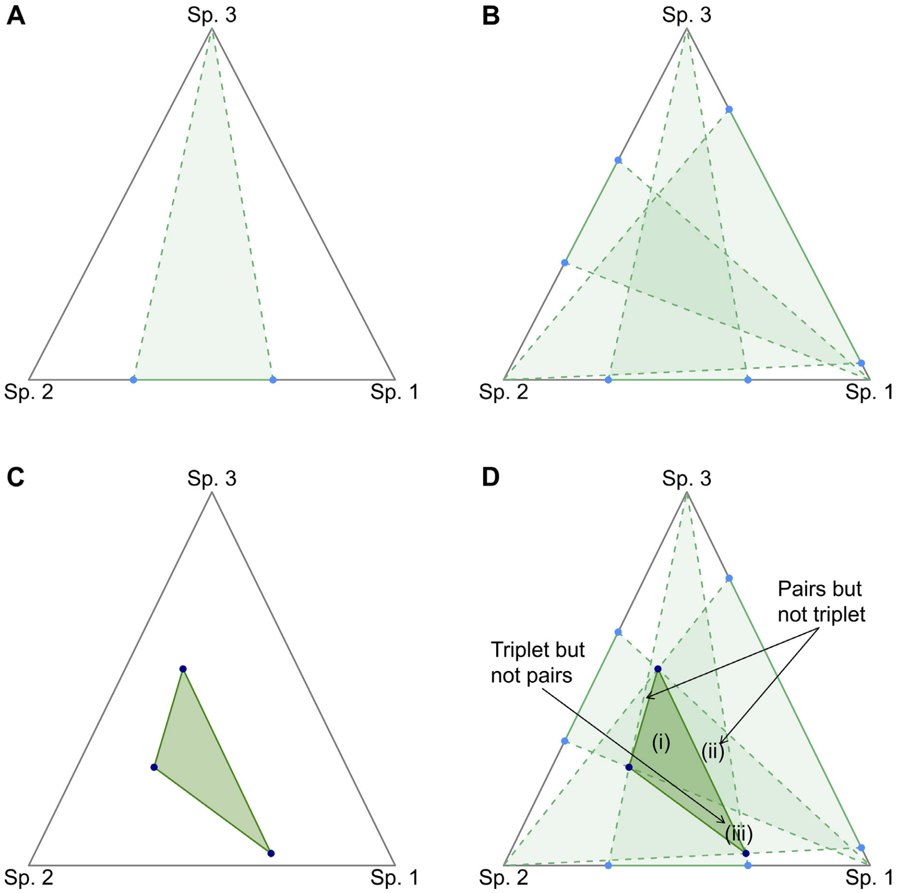

FIG. 6. Community vs. pairwise effects on coexistence. Panel A depicts the feasibility domain of the pair formed by species 1 and 2 (D_{12}). If one chooses a vector of intrinsic growth rates inside the green triangle, then in absence of species 3, species 1 and 2 will coexist. Panel B shows the three 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_{all}). 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. [Color figure can be viewed at wileyonlinelibrary.com]

coexistence of all pairs (D_{all}) vs. 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, $D_{\mathrm{all}} \cap D_{\mathrm{F}} \neq \varnothing$); (ii) all pairs show coexistence but not the triplet (the region of D_{all} not overlapping with D_{F}); (iii) not all pairs show coexistence but the triplet does (the region of D_{F} not 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 (Fig. 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 Fig. 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 Fig. 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 ($D_{\mathrm{all}} = \varnothing$). 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

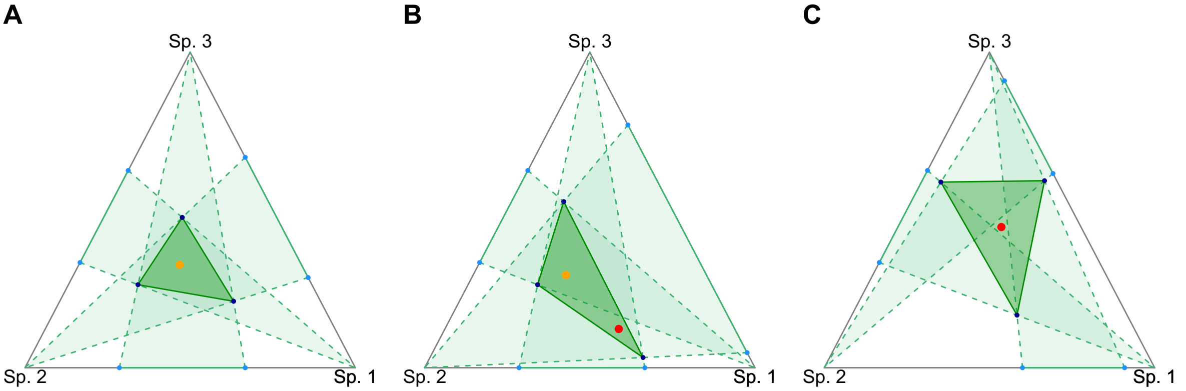

FIG. 7. Three general cases of community and pairwise coexistence. Panel A shows an example where the feasibility domain of the triplet (D_{F}) is completely inside the pairwise coexistence domain (D_{all}). If the vector of intrinsic growth rates is located at the orange dot, each pair coexists in isolation 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 ($D_{\mathrm{all}} = \varnothing$). 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. [Color figure can be viewed at wileyonlinelibrary.com]

pairwise 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 pairwise 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 pairwise 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 ($\varDelta$), 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 vs. that allowing the coexistence of all pairs. Mathematically, this is given by $\varDelta = \varOmega - \varOmega_{\text{all}}$, where $\varOmega$ is the structural analog of niche difference and $\varOmega_{\text{all}}$ is the fraction of intrinsic demographics compatible with the coexistence of all pairs in the community. We calculated $\varOmega_{\text{all}}$ 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 Fig. 7C), a negative value indicates less opportunities for coexistence (as in Fig. 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 Fig. 7A, whereas a value of zero would indicate no overlap as in the case of Fig. 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 ($\varDelta$), 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, 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, USA. 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 ($\boldsymbol{\alpha}$), 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. 2017*a*).

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 ($\varDelta$) 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, Fig. 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 (Fig. 8A) or not overlap (Fig. 8B) 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 ($\Delta \approx 0$; Fig. 9A). 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.

Fig. 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 ($\omega > 0$), only in about 15% of triplets and <5% of quadruplets this

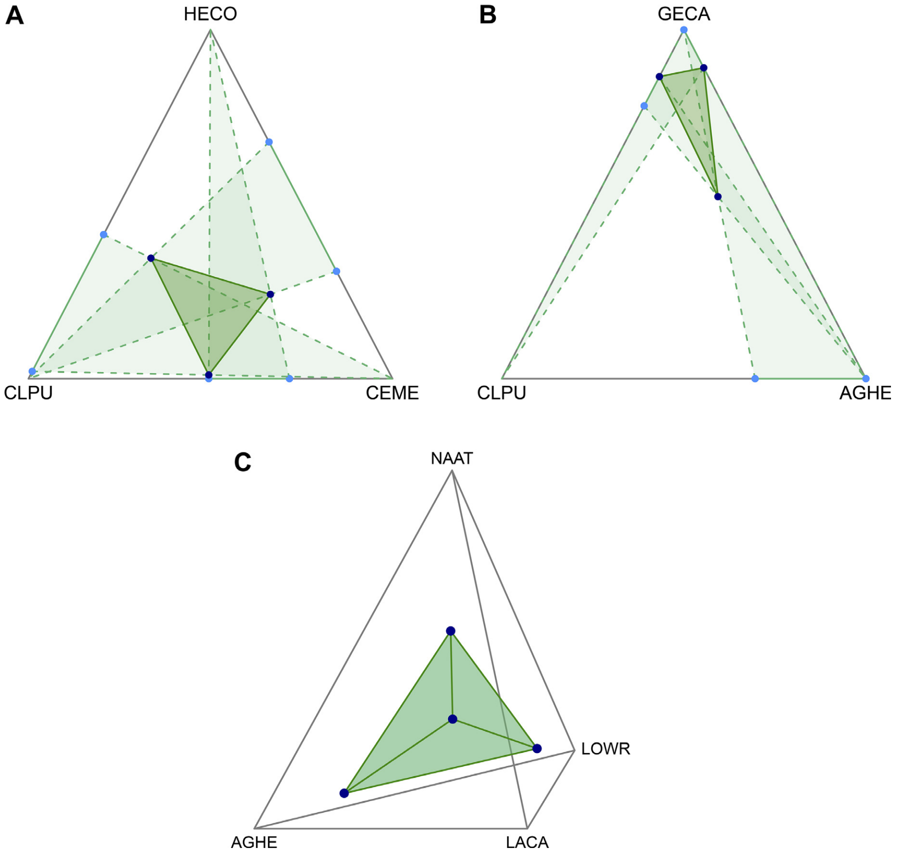

FIG. 8. Illustration of feasibility domains for triplets and quadruplets of annual plant species in a California field system. Panels A and B show the feasibility domains for two triplets, and Panel C for a quadruplet based on the empirically measured interaction coefficients (Godoy et al. 2014, Kraft et al. 2015). These feasibility domains are all projected on a unit simplex as shown for artificially constructed interaction matrices in Figs. 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). [Color figure can be viewed at wileyonlinelibrary.com]

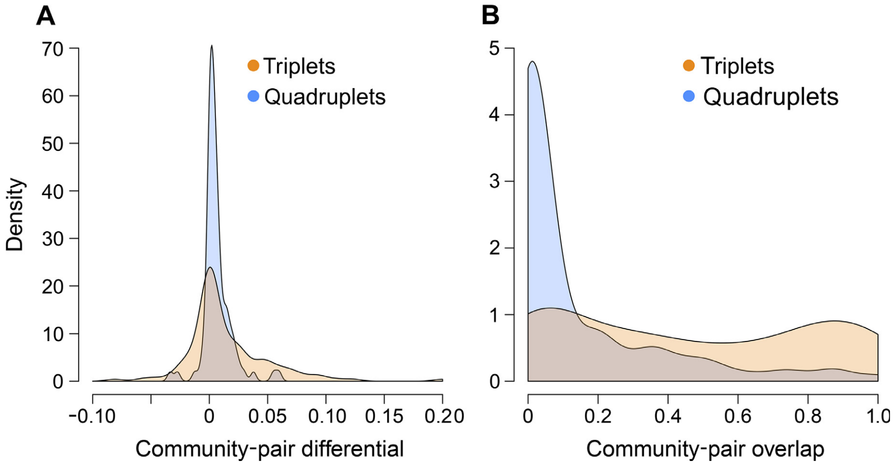

Fig. 9. Quantifying the sources of multispecies coexistence in annual plant assemblages. For fitted competition coefficients obtained in an annual plant system (Godoy et al. 2014, Kraft et al. 2015), panels A and B show the community-pair differential (Δ) and the community-pair overlap (ω), respectively. 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. [Color figure can be viewed at wileyonlinelibrary.com]

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.

Discussion

Understanding 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 (Logofet 1993, Hofbauer and Sigmund 1998), 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 two-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 (Yodzis 1988, Wootton 1993), and classic theory can be used to evaluate how the 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 Figs. 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. 2016*a, 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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Literature Cited

Adler, P. B., J. HilleRisLambers, and J. M. Levine. 2007. A niche for neutrality. Ecology Letters 10:95–104.

Allesina, S., and J. M. Levine. 2011. A competitive network theory of species diversity. Proceedings of the National Academy of Sciences of the United States of America 108:5638–5642.

Angert, A. L. 2009. The niche, limits to species' distributions, and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. Proceedings of the National Academy of Sciences 106:19693–19698.

Barabás, G., M. J. Michalska-Smith, and S. Allesina. 2016. The effect of intra- and interspecific competition on coexistence in multispecies communities. American Naturalist 188(1):E1–E12. https://doi.org/10.1086/686901.

Bastolla, U., M. L assig, S. C. Manrubia and A. Valleriani. 2005. Biodiversity in model ecosystems, I: coexistence conditions for competing species. Journal of Theoretical Biology 235:521–530.

Bastolla, U., M. A. Fortuna, A. Pascual-García, A. Ferrera, B. Luque, and J. Bascompte. 2009. The architecture of mutualistic networks minimizes competition and increases biodiversity. Nature 458:1018–1020.

Billick, I., and T. J. Case. 1994. Higher order interactions: what are they and how can they be detected? Ecology 65:1–13.

Carroll, I. T., J. B. Cardinale, and R. M. Nisbet. 2011. Niche and fitness differences relate the maintenance of diversity to ecosystem function. Ecology 92:1157–1165.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proceedings of the National Academy of Sciences of the United States of America 87:9610–9614.

Case, T. J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press, Oxford, UK.

Chesson, P. 1990. MacArthur's consumer–resource model. Theoretical Population Biology 37:26–38.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:346–366.

Chesson, P. 2003. Quantifying and testing coexistence mechanisms arising from recruitment fluctuations. Theoretical Population Biology 64:345–357.

Chesson, P. 2012. Species competition and predation. Pages 10061–10085 in R. A. Meyers, editor. Encyclopedia of Sustainability Science and Technology. Volume 14. Springer, New York, New York, USA.

Chesson, P., and J. J. Kuang. 2010. The storage effect due to frequency-dependent predation in multispecies plant communities. Theoretical Population Biology 78:148–164.

Chu, C., and P. B. Adler. 2015. Large niche differences emerge at the recruitment stage to stabilize grassland coexistence. Ecological Monographs 85:373–392.

Darwin, C. R. 1859. On the Origin of Species. John Murray, London, UK.

Edwards, K. F., and S. J. Schreiber. 2010. Preemption of space can lead to intransitive coexistence of competitors. Oikos 119:1201–1209.

Godoy, O., N. J. B. Kraft, and J. M. Levine. 2014. Phylogenetic relatedness and the determinants of competitive outcomes. Ecology Letters 17:836–844.

Godoy, O., N. J. B. Kraft and J. M. Levine. 2017*a*. Dataset Godoy et al. 2014 Ecology Letters. https://doi.org/10.6084/m9.figshare.4793488.v1.

Godoy, O., D. B. Stouffer, J. B. N. Kraft, and J. M. Levine. 2017*b*. Intransitive in infrequent and fails to promote coexistence without niche differences. Ecology 98:1193–1200. https://doi.org/10.1002/ecy.1782.

Hofbauer, J., and K. Sigmund. 1998. Evolutionary Games and Population Dynamics. Princeton University Press, Princeton, New Jersey, USA.

Holt, G., and P. Chesson. 2014. Variation in moisture duration as a driver of coexistence by the storage effect in desert annual plants. Theoretical Population Biology 92:36–50.

Hubbell, S. P. 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, New Jersey, USA.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist 95:137–145.

Kerr, B., M. A. Riley, M. W. Feldman, and B. J. M. Bohannan. 2002. Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. Nature 418:171–174.

Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. Proceedings of the National Academy of Sciences 112:797–802.

Levine, S. H. 1976. Competitive interactions in ecosystems. American Naturalist 110:903–910.

Levine, J. M., and J. HilleRisLambers. 2009. The importance of niches for the maintenance of species diversity. Nature 461:254–257.

Logofet, D. O. 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press, Boca Raton, FL.

Logofet, D. O. 2005. Stronger-than-Lyapunov notions of matrix stability, or how flowers help solve problems in mathematical ecology. Linear Algebra and its Applications 398:75–100.

Lotka, A. J. 1932. The growth of mixed populations: two species competing for a common food. Journal of Washington Academy of Sciences 21:461469.

May, R. M. 1971. Stability in multispecies community models. Mathematical Biosciences 12:59–79.

May, R. M. 1972. Will a large complex system be stable? Nature 238:413–414.

May, R. M., and W. J. Leonard. 1975. Nonlinear aspects of competition between three species. SIAM Journal on Applied Mathematics 29:243–253.

Roberts, A. 1974. The stability of a feasible random ecosystem. Nature 251:607–608.

Rohr, R. P., S. Saavedra, and J. Bascompte. 2014. On the structural stability of mutualistic systems. Science 345:1253497.

Rohr, R. P., S. Saavedra, G. Peralta, C. M. Frost, L.-F. Bersier, J. Bascompte, and J. M. Tylianakis. 2016. Persist or produce: a community trade-off tuned by species evenness. American Naturalist 188:411–422.

Saavedra, S., R. P. Rohr, L. J. Gilarranz, and J. Bascompte. 2014. How structurally stable are global socioeconomic systems? Journal of the Royal Society, Interface 11:20140693.

Saavedra, S., R. P. Rohr, M. A. Fortuna, N. Selva, and J. Bascompte. 2016*a*. Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. Ecology 94:865–873.

Saavedra, S., R. P. Rohr, J. M. Olesen and J. Bascompte. 2016*b*. Nested species interactions promote feasibility over stability during the assembly of a pollinator community. Ecology and Evolution 97:865–887 https://doi.org/10.1002/ece3.1930.

Saavedra, S., R. P. Rohr, J. Bascompte, O. Godoy, N. J. B. Kraft, and J. M. Levine. 2017. Data from: a structural approach for understanding multispecies coexistence. Dryad Digital Repository. https://doi.org/10.5061/dryad.v9f5s.

Spiesman, B. J., and B. D. Inouye. 2015. The consequences of multiple indirect pathways of interaction for species coexistence. Theoretical Ecology 8:225. https://doi.org/10.1007/s12080-014-0246-4.

Stone, L. 1988. PhD Thesis: Some problems of community ecology: processes, patterns, and species persistence in ecosystems. Dissertation. Monash University.

Stump, S. M., and P. Chesson. 2015. Distance-responsive predation is not necessary for the Janzen-Connell hypothesis. Theoretical Population Biology 11:60–70.

Svirezhev, Y. M. and D. O. Logofet. 1983. Stability of Biological Communities. Mir Publishers, Moscow.

Takeuchi, Y. 1996. Global Dynamical Properties of Lotka-Volterra Systems. World Scientific, Singapore.

Thom, R. 1972. Stabilité Structurelle et Morphogenèse. InterÉditions, Paris, France.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, New Jersey, USA.

Vandermeer, J. H. 1969. The competitive structure of communities: an experimental approach with protozoa. Ecology 50:362–371.

Vandermeer, J. H. 1970. The community matrix and the number of species in a community. American Naturalist 104:73–83.

Vandermeer, J. H. 1975. Interspecific competition: a new approach to the classical theory. Science 188:253–255.

Volterra, V. 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris, France.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 74:195–206.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology 69: 508–515.

SUPPORTING INFORMATION

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Appendix S1: Invasion criterion

One of the most useful criteria for understanding multispecies coexistence has been based on the notion of species invasion (Case, 1990, 2000). The invasion criterion establishes that if in a community of n-species, each species can be removed, reintroduced into the sub-community of $n-1$ species, and grow, then species coexistence is guaranteed (Case, 2000). Mathematically, the condition for species i to invade the sub-community of $n-1$ species is given by the invasion growth rate r_i^{inv}. For the Lotka Volterra model defined in the main text, let $\boldsymbol{r}$ be the vector of intrinsic growth rates and $\boldsymbol{\alpha}$ the matrix of competition coefficients of a given set of n-species. Let us assume that species i is depressed to the limit at which its abundance is zero. Then the abundances, if positive, of the $n-1$ remaining species are given by the following vector

$$\tilde{\boldsymbol{N}}_{\boldsymbol{-i}} = (\boldsymbol{\alpha}_{\boldsymbol{-i,-i}})^{-1}\boldsymbol{r}_{\boldsymbol{-i}}, \tag{S1}$$

where $\boldsymbol{\alpha}_{\boldsymbol{-i,-i}}$ is the interaction matrix without row and column i, and $\boldsymbol{r}_{\boldsymbol{-i}}$ is the vector of intrinsic growth rates without the element i. Assuming that the abundances of the $n-1$ species are positive, i.e., $(\tilde{N}_{-i})_j > 0$ for each species j, the invasion growth rate of species i then can be defined by

$$r_i^{\text{inv}} = r_i - \sum_k (\boldsymbol{\alpha}_{\boldsymbol{i,-i}})_k (\tilde{\boldsymbol{N}}_{\boldsymbol{-i}})_k, \tag{S2}$$

where $\boldsymbol{\alpha}_{\boldsymbol{i,-i}}$ is the row i of the matrix of competition coefficients without the column i. Biologically, the invasion growth rate corresponds to the per capita growth of species i when completely depressed, and it shows that species i can invade the community if the invasion growth rate is positive, i.e., $r_i^{\text{inv}} > 0$. Assuming that the competition system is globally stable, and that each species can invade, then it is clear that this criterion does grant the coexistence of the n-species community. Note, however, that the invasion criterion defined above needs as a prerequisite the coexistence of all the combinations of $n-1$ species (i.e., for all cases the solution of Equation S1 has to be positive). This prerequisite is always true for 2-species communities (if one species goes extinct then the other one will always persist).

Importantly, the invasion criterion guarantees multispecies coexistence in the classical Lotka-Volterra competition model. That is, let $\boldsymbol{\alpha}$ be the interaction competition matrix of a community of n species, and let us assume that this matrix of competition coefficients is either positive definite or Volterra-dissipative, i.e., globally stable. Any sub-matrix of a positive definite or Volterra-dissipative matrix is again positive definite or Volterra-dissipative (Logofet, 1993). Biologically, this means that the global stability property is conserved when looking at a sub-community. Additionally, the invasion criterion assumes that all the n sub-communities of $n-1$ species are feasible. This implies that an equilibrium point with fewer species in one of the $n-1$ sub-communities is automatically unstable. The opposite would be in contradiction to the assumption that the sub-communities of $n-1$ are all feasible. Similarly, the invasion criterion assumes that the invasion growth rates are positive for all species. This implies that the n feasible equilibria with $n-1$ are all unstable. Therefore, the only possibility is the existence of a feasible and stable equilibrium point for the entire community. This proves that the invasion criterion is a sufficient condition for multispecies coexistence (Case, 2000). In fact, the invasion criterion can be thought of as a sufficient condition for short-term species permanence (Jansen and Sigmund, 1998). Yet, this criterion does not apply any more in the case where at least one of the $n-1$ sub-communities is not feasible.

Note that the invasion criterion needs as a prerequisite the coexistence of all the combinations of $n-1$ species (i.e., for all cases the solution of Equation S1 has to be positive). This prerequisite is always true for 2-species communities (if one species goes extinct then the other one will always persist). For 3-species communities, this will imply that the region of triplet coexistence (Ω) always has to be inside the region of pairwise coexistence (Ω_{all}). Figure 7A illustrates this case. If the set of intrinsic growth rates is located anywhere inside the dark region (e.g., orange point), each individual species can be removed (the other two species will coexist as defined by their region of pairwise coexistence), and reintroduced (the triplet will coexist as defined by the darker region).

However, Figure 7B illustrates a scenario where the region of triplet coexistence does not fall 100% inside the region of overlap of pairwise coexistence (similar to the case shown in Figure 6D). Importantly, if the set of intrinsic growth rates is located at the orange point (inside the region of overlap), the invasion criterion applies just as in the case above. 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 species 1 and 2 in isolation (left side).

An extreme case showing that the invasion criterion is not a necessary condition for species coexistence is the rock-paper-scissors dynamic, whose feasibility domain is illustrated in Figure 7C. Here, the domain of coexistence of the three pairs of species does not intersect (the pairwise domain does not exit). If one chooses a vector of intrinsic growth rates in the middle of the darker region (red point), species 3 out-competes 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 out-competes 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 out-competes 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). Therefore the coexistence of the triplet only emerges from a mechanism other than pairwise coexistence—rock-paper-scissors competition in this case. Overall, an invasion condition based on one species invading the other two does not entirely capture the potential for coexistence (Case, 2000). This potential emerging from simple population dynamics can only be seen by moving from an algebraic into a structural approach.

References

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. Proc. Natl. Acad. Sci. U.S.A. **87**:9610–9614.

Case, T. J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press.

Jansen, V. A., and K. Sigmund. 1998. Shaken not stirred: on permanence in ecological communities. Theoretical Population Biology **54**:195–201.

Logofet, D. O. 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press.

Appendix S2: Coexistence defined by community persistence and permanence

The ecological concept of species coexistence is broad and several important but not necessarily equivalent definitions have been proposed (Hofbauer and Sigmund, 1998). Generally, coexistence is taken to mean the persistence of all species, which implies that species abundances should be strictly positive over the long term (Hofbauer and Sigmund, 1998). However, this definition of coexistence does not exclude the possibility that the trajectories of species abundances, defined by the dynamical system, could transiently approach zero for one or more species. In such cases, a small perturbation can push species towards extinction. Therefore, a system is called "permanent" if all trajectories remain bounded away from zero, i.e., the abundances never go below and above some positive thresholds (Hofbauer and Sigmund, 1998). Thus species permanence is a stronger condition than species persistence for coexistence. With the structural approach to species coexistence developed, we investigate the necessary condition for permanence, and the necessary and sufficient condition for persistence: that is the existence of a feasible and globally stable equilibrium point.

Unfortunately, sufficient conditions for permanence in systems with more than three species are not known (Hofbauer and Sigmund, 1998). However, global stability of a feasible (as defined in the text) equilibrium point is a sufficient condition for species persistence (Svirezhev and Logofet, 1983; Logofet, 1993, 2005; Rohr et al., 2014; Saavedra et al., 2016*b*,*a*), and conditions for global stability have been studied intensively during the past decades (summarized in Appendix S3). Importantly, in many cases, global stability conditions can be deduced directly from the matrix of competition coefficients, and do not involve the intrinsic growth rates. For example, matrices of pairwise interactions as derived from a niche overlap framework (termed "dissipative" (Volterra, 1931) are always globally stable (Svirezhev and Logofet, 1983; Logofet, 1993, 2005). Therefore, to investigate species coexistence in this manuscript we focus mostly on feasibility explicitly assuming that global stability is satisfied.

The conditions for global stability in a matrix of competition coefficients are described in Appendix S3, but we note that even if we instead focus on a local stability condition, our results remain largely the same for most models of competing species. Note that feasibility is a necessary condition for permanence and persistence, while global stability is a sufficient condition for persistence once feasibility conditions are fulfilled. Therefore, our structural approach can provide the necessary conditions for species coexistence regardless of whether the systems is stable or not.

References

Hofbauer, J., and K. Sigmund. 1998. Evolutionary Games and Population Dynamics. Princeton Univ. Press.

Logofet, D. O. 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press.

Logofet, D. O. 2005. Stronger-than-Lyapunov notions of matrix stability, or how flowers help solve problems in mathematical ecology. Linear Algebra and its Applications **398**:75–100.

Rohr, R. P., S. Saavedra, and J. Bascompte. 2014. On the structural stability of mutualistic systems. Science **345**:1253497.

Saavedra, S., R. P. Rohr, M. A. Fortuna, , N. Selva, and J. Bascompte. 2016*a*. Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. Ecology **94**:865–873.

Saavedra, S., R. P. Rohr, J. M. Olesen, and J. Bascompte. 2016*b*. Nested species interactions promote feasibility over stability during the assembly of a pollinator community. Ecology and Evolution page 10.1002/ece3.1930.

Svirezhev, Y. M., and D. O. Logofet. 1983. Stability of Biological Communities. Mir Publishers.

Volterra, V. 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris.

Appendix S3: Short review of stability analysis

In this appendix we present a short review about the mathematical results about the stability of feasible equilibrium points for ordinary differential equations of the form $\frac{dN_i}{dt} = N_i f_i(\boldsymbol{N})$. We recall that an equilibrium point (N_i^*) is called feasible when it satisfies both the condition $f_i(\boldsymbol{N}^*) = 0$ and $N_i^* > 0$ for all species i. The theory presented here is part of classic results that can be found in the following references (Volterra, 1931; Johnson, 1974; Goh, 1977; Svirezhev and Logofet, 1983; Hofbauer and Sigmund, 1998; Logofet, 1993; Takeuchi, 1996; Logofet, 2005).

For instance, a given equilibrium point is locally stable if any small perturbation in the population size of species is absorbed, and the system eventually returns to its equilibrium point. A stronger dynamical stability condition is global stability. Global stability implies that the equilibrium point is a global attractor and that the trajectories of the dynamical system converge to the equilibrium regardless of their starting point. Global stability is conventionally derived from a Lyapunov function (Goh, 1977; Logofet, 1993).

The condition for local stability of an equilibrium point is encapsulated in the so-called Jacobian matrix ($\mathbf{J}$), which is evaluated at the equilibrium point (Case, 2000; Strogatz, 2001). We recall that the Jacobian matrix is made of the partial derivative of the right side of the differential equation, i.e., $J_{ij} = \frac{\partial N_i f_i(\boldsymbol{N})}{\partial N_j}$. Evaluated at a feasible equilibrium point N_i^*, the Jacobian matrix reads,

$$J_{ij} = N_i^* \frac{\partial f_i(\boldsymbol{N})}{\partial N_j}|_{\boldsymbol{N}=\boldsymbol{N}^*}.$$

The classic results in dynamical systems state that an equilibrium point is locally stable (i.e., the system return to its equilibrium point after infinitesimal small perturbation) if all the eigenvalues of the Jacobian matrix have negative real parts (or positive real parts if the negative sign is written in front of the matrix of competition coefficients) (Case, 2000; Strogatz, 2001). If one assumes a linear function for the per capita growth functions $f_i = r_i - \sum_j \alpha_{ij} N_j$, then the Jacobian matrix is given by $J_{ij} = -N_i^* \alpha_{ij}$. The Jacobian informs only about the local stability of the equilibrium point at which it has been evaluated. However, here we are not only interested in one particular equilibrium point and whether it is locally stable, but we are interested in assessing the global stability of any feasible equilibrium point.

From now on, we assume that the per capita growth rate is a linear function, and therefore, the dynamical system is given by the generalized Lotka-Volterra model, $\frac{dN_i}{dt} = N_i(r_i - \sum_j \alpha_{ij} N_j)$. As shown above, the elements of the Jacobian matrix are a function of both the interaction strength (α_{ij}) and the equilibrium point $(N_i^* > 0)$. Therefore, for a given interaction matrix $\boldsymbol{\alpha}$, the eigenvalues of the Jacobian matrix are function of the specific value of the equilibrium point. This implies, that in theory, it is possible to have an equilibrium point that is locally stable, while another equilibrium point is unstable for the same matrix of competition coefficients. To overcome this problem, one can use the concept of D-stability (Johnson, 1974; Svirezhev and Logofet, 1983; Logofet, 1993, 2005). A matrix is called D-stable if its eigenvalues have positive real parts when the matrix is multiplied from the left by any positive diagonal matrix. Thus, if the matrix of competition coefficients $\boldsymbol{\alpha}$ is D-stable, this condition grants the local stability of any feasible equilibrium point.

The notion of D-stability grants the local stability of any feasible equilibrium point, however, it does not grant global stability. By global stability of a feasible equilibrium we mean that all the trajectories of the dynamical system converge to that equilibrium point independently of the initial conditions, assuming they are positive (Volterra, 1931; Goh, 1977; Svirezhev and Logofet, 1983; Hofbauer and Sigmund, 1998; Logofet, 1993; Takeuchi, 1996; Logofet, 2005). A sufficient condition that implies global stability is for a matrix to be Volterra-dissipative. A matrix $\boldsymbol{A}$ is Volterra-dissipative if there exist a positive diagonal matrix $\boldsymbol{D}$ such that the matrix $\boldsymbol{D}\boldsymbol{A} + \boldsymbol{A}^t\boldsymbol{D}$ is positive definite (all the eigenvalues are positive). It has been proved that if the matrix of competition coefficients $\boldsymbol{\alpha}$ is Volterra-dissipative then any feasible equilibrium is globally stable. One can even prove that if the matrix of competition coefficients $\boldsymbol{\alpha}$ is Volterra-dissipative then there exists a unique global stable equilibrium point, which is not necessarily feasible (some species may go extinct).

Volterra-dissipative matrices imply D-stability, which in turn implies that all the eigenvalues of the interaction matrix have real positive parts (Svirezhev and Logofet, 1983; Logofet, 1993, 2005). In general it is difficult to test whether a matrix is Volterra-dissipative. However, for some classes of matrices we have analytic results. For example if the matrix of competition coefficients is derived from species distances in a niche space, then this matrix is automatically Volterra-dissipative (MacArthur and Levins, 1967; Logofet, 1993). One can test whether a matrix is Volterra-dissipative by testing if it is positive definite. A matrix $\boldsymbol{A}$ is positive definite if the eigenvalues of its symmetrization $(\boldsymbol{A} + \boldsymbol{A}^t)$ are positive. A positive definite matrix is automatically Volterra-dissipative, however, a Volterra-dissipative is not necessarily positive definite. Positive definite is in general a very strong condition on a matrix.

The above notions of stability assume a linear function for the per capita growth rate $(f_i(\boldsymbol{N}))$, i.e., a generalized Lotka-Volterra model. In the following we present a mathematical result that generalizes the concept of Volterra-dissipative to nonlinear functions for the per capita growth rate (f_i) (Goh, 1977). We introduce the matrix of the partial derivative of the functions f_i:

$$\alpha_{ij}(\boldsymbol{N}) = \frac{\partial f_i(\boldsymbol{N})}{\partial N_j}.$$

This matrix is function of abundances $\boldsymbol{N}$ and can intuitively be interpreted as the linearized interaction strength at the point $\boldsymbol{N}$. If there exists a positive diagonal matrix $\boldsymbol{D}$ such that $\boldsymbol{D}\boldsymbol{\alpha}(\boldsymbol{N}) + \boldsymbol{\alpha}(\boldsymbol{N})^t\boldsymbol{D}$ is positive definite for any positive value of $\boldsymbol{N} > 0$, then a feasible equilibrium is globally stable. Note that the diagonal matrix $\boldsymbol{D}$ has to be independent of the point $\boldsymbol{N}$. The difficulty is to find the diagonal matrix D, however, if the matrix $\alpha_{ij}(\boldsymbol{N})$ is positive definite for any value of $\boldsymbol{N}$ then a feasible equilibrium is globally stable.

References

Case, T. J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press.

Goh, B. S. 1977. Global Stability in Many-Species Systems. Am. Nat. **111**:135–143.

Hofbauer, J., and K. Sigmund. 1998. Evolutionary Games and Population Dynamics. Princeton Univ. Press.

Johnson, C. R. 1974. Sufficient conditions for D-Stability. J. Econom. Theory **9**:53–62.

Logofet, D. O. 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press.

Logofet, D. O. 2005. Stronger-than-Lyapunov notions of matrix stability, or how flowers help solve problems in mathematical ecology. Linear Algebra and its Applications **398**:75–100.

MacArthur, R., and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat **101**:377–385.

Strogatz, S. H. 2001. Nonlinear Dynamics and Chaos. Westview press.

Svirezhev, Y. M., and D. O. Logofet. 1983. Stability of Biological Communities. Mir Publishers.

Takeuchi, Y. 1996. Global dynamical properties of Lotka-Volterra systems. World Scientific.

Volterra, V. 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris.

Appendix S4: Examples of dynamical models to which our structural framework can be applied

In this appendix we provide four examples of dynamical systems describing the competition among species to which the structural framework apply (Volterra, 1931; Case, 2000; Brauer and Castillo-Chavez, 2012). The two first examples are time continuous models given by ordinary differential equation. The other two examples are time discrete models and therefore are described by difference equations.

Competition Lotka-Volterra model

The competition Lotka-Volterra model is given by the following ordinary differential equation (Volterra, 1931; Case, 2000; Brauer and Castillo-Chavez, 2012):

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

The parameters of the model correspond to the intrinsic growth rate ($r_i > 0$) of species i, and the competition interaction strength ($\alpha_{ij} > 0$) between species i and j. The structural framework for the niche and fitness difference applies directly to the model, and all these quantities (Equations 13 to 15) can be computed directly. The global stability condition is determined by assuming that the matrix of competition coefficients ($\boldsymbol{\alpha}$) is Volterra-dissipative (see Appendix S3).

Saturating competition model

This is a modification of the Lotka-Volterra model by assuming a non-linear function for the per capita growth rates (Brauer and Castillo-Chavez, 2012). For this model we assume that the negative effect of the competition is achieved trough a saturating function. The model is given by the following ordinary differential equation:

$$\frac{dN_i}{dt} = N_i \left(-\mu_i + \frac{\nu_i}{1 + \sum_{j=1}^{n} \tilde{\alpha}_{ij} N_j} \right)$$

The parameters of the model correspond to the demographic parameters ($\mu_i > 0$ and $\nu_i > 0$) of species i, and the competition interaction ($\tilde{\alpha}_{ij} > 0$) between species i and j. To apply the structural framework to this model we need first to derive the equation for a feasible equilibrium. A feasible equilibrium $\boldsymbol{N}^*$ corresponds to the solution of

$$-\mu_i + \frac{\nu_i}{1 + \sum_{j=1}^{n} \tilde{\alpha}_{ij} N_j^*} = 0$$

for all species i. By manipulating this equation we arrive at the following linear equation

$$\nu_i - \mu_i = \sum_{j=1}^{n} \mu_i \tilde{\alpha}_{ij} N_j^*.$$

By identifying $r_i = \nu_i - \mu_i$ and $\alpha_{ij} = \mu_i \tilde{\alpha}_{ij}$, we can apply the structural framework (Equations 13 to 15). The stability condition for the model can be derived as follow. As explained in Appendix S3, we compute the partial derivative of the per capita growth functions. They are given by

$$\alpha_{ij}(\boldsymbol{N}) = \frac{\nu_i \tilde{\alpha}_{ij}}{(1 + \sum_{j=1}^{n} \tilde{\alpha}_{ij} N_j)^2}.$$

If the matrix $\tilde{\boldsymbol{\alpha}}$ is derived from a niche overlap framework, then this implies that the matrix of partial derivatives $(\alpha_{ij}(\boldsymbol{N}))$ is positive definite for any value of $\boldsymbol{N} > 0$, and therefore, this grants the global stability of any feasible equilibrium point.

Time discrete Lotka-Volterra model

The time discrete version of the competition Lotka-Volterra model is given by the following difference equation (Case, 2000; Brauer and Castillo-Chavez, 2012):

$$N_{i,t+1} = N_{i,t} e^{\left(r_i - \sum_{j=1}^{S} \alpha_{ij} N_j\right)}.$$

The state variable $N_{i,t}$ denotes the abundance (or biomass) of species i at time t. The parameters of the model correspond to the intrinsic growth rates (r_i) of species i, and the competition interaction strength (α_{ij}). Similarly to the time continuous model, the structural framework (Equations 13 to 15) applies directly. The stability condition is more difficult to derive. Indeed, even if the matrix of competition coefficients $\boldsymbol{\alpha}$ is positive definite or Volterra-dissipative and there exists a feasible equilibrium point, depending on the level of intrinsic growth rate, the model may exhibit cyclic and chaotic behavior. This phenomenon is known as the doubling-period.

Annual plant model

The annual plant model is a time discrete model that describes the dynamic of seed banks. The state variable $N_{i,t}$ corresponds to the seed bank of plant species i at time t. The model is given by the following difference equation (Chesson, 1990):

$$N_{i,t+1} = (1 - g_i)\, s_i N_{i,t} + \frac{g_i \lambda_i N_{i,t}}{1 + \sum_{j=1}^{n} \tilde{\alpha}_{ij} g_j N_{j,t}}.$$

The parameters correspond to the germination rate ($0 < g_i < 1$), the seed survival probability ($0 < s_i < 1$), the fecundity rate (λ_i), and the competition strength ($\tilde{\alpha_{ij}}$). To apply the structural framework, we first need to derive the equations determining the feasible equilibrium $\boldsymbol{N}^* > 0$. A feasible equilibrium has to be the solution of the equation $(1-g_i)\,s_i + \frac{g_i\lambda_i}{1+\sum_{j=1}^{n}\tilde{\alpha}_{ij}g_jN_j^*} = 1$ for all species i. By manipulating this equation we can derive the following linear equation:

$$\frac{g_i\lambda_i}{1-(1-g_i)s_i} - 1 = \sum_{j=1}^{n}\tilde{\alpha}_{ij}g_jN_j^*.$$

By identifying $r_i = \frac{g_i\lambda_i}{1-(1-g_i)s_i} - 1$ and $\alpha_{ij} = \tilde{\alpha}_{ij}g_j$, we can apply the structural framework (Equations 13 to 15). The stability conditions are difficult to derive analytically. Numerical simulations tend to suggest that if the matrix of competition coefficients $\tilde{\boldsymbol{\alpha}}$ is positive definite or Volterra-dissipative then a feasible equilibrium is globally stable. However, there has been no proofs showing the conditions for global stability in multispecies systems.

References

Brauer, F., and C. Castillo-Chavez. 2012. Mathematical Models in Population Biology and Epidemiology, 2nd edition. Springer.

Case, T. J. 2000. An Illustrated Guide to Theoretical Ecology. Oxford University Press.

Chesson, P. 1990. Geometry, Heterogeneity and Competition in Variable Environments. Philosophical Transactions of the Royal Society of London B: Biological Sciences **330**:165–173.

Volterra, V. 1931. Leçons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris.

Appendix S5: Differences between the MCT and the structural framework for 2-species coexistence

The structural approach and MCT framework quantify niche and fitness differences in a slightly different way. MCT's framework incorporates the competitive imbalance between two competitors, by multiplying each term of the inequality (Equ. 3) by $\sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}}$, while the structural approach quantifies directly the solid angle defined by the same inequality (Equ. 3). Therefore, MCT's niche difference can be seen as the structural analog of niche difference after removing the effects of the competitive imbalance. In the MCT approach, removing the effects of the competitive imbalance has the advantage of revealing the dominant competitor when the niche difference is zero.

Figure S1 shows two extreme cases illustrating the subtle but fundamental difference between MCT's and the structural frameworks. Specifically, the top panels (**A-C**) show that if the position of the feasibility domain (area formed by the inequalities) changes due to a changing competitive imbalance, a compensatory increase in the MCT niche difference is required to yield the same structural analog of niche difference Ω. Similarly, the bottom panels (**D-E**) show that if one interspecific competition coefficient equals zero (i.e., one of the slopes lies on the border) any niche difference less than 1 will allow coexistence under MCT. By contrast, the structural approach is a geometric approach that quantifies the set of intrinsic growth rates leading to coexistence independent of whether the competition among species is balanced (and gives different Ω in the two cases depicted in panels d and e). Note that only the structural approach has a probabilistic interpretation. Indeed the structural-based measure of niche difference Ω gives the probability of having a feasible system, i.e., it is the probability of sampling a set of growth rates in the feasibility domain (assuming that the growth rates are sampled uniformly but with a fixed norm, where the direction of the vector of growth rates is sampled uniformly).

We may wonder if there is a way to incorporate the competitive imbalance into the structural approach. To do this, we first need to understand from where this fundamental difference is arising. MCT's niche difference is deduced from the two inequalities (2), which give the condition of coexistence (assuming the stability condition satisfied). The two inequalities (2) are then combined into Equation (3), which describes the upper and lower bound that the ratio in intrinsic growth rates can tolerate to ensure coexistence. Then the competitive imbalance term is incorporated by multiplying each term of Equation (3) by the factor $\sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}}$. This leads to the classical definition of niche difference (Equ. 4).

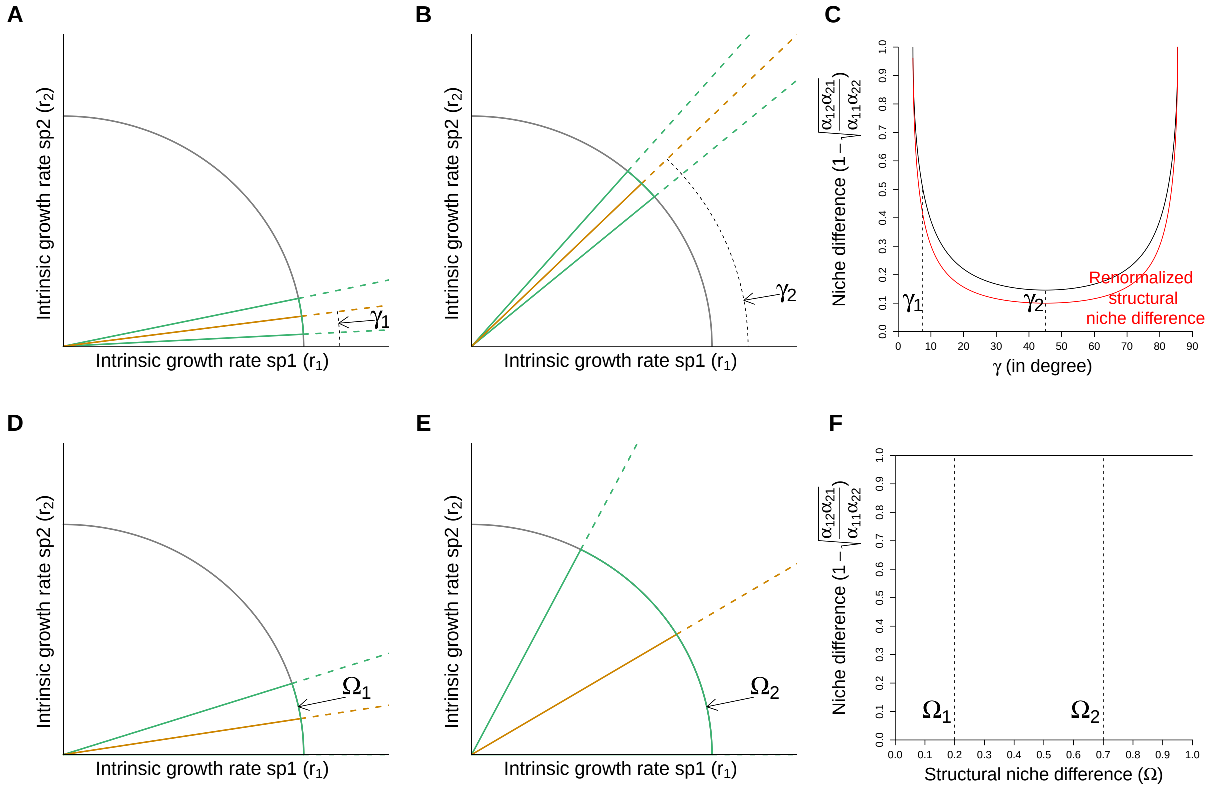

Figure S1: **Differences between the MCT and the structural approaches.** Panels **A** and **B** show the same area (Ω) between the two inequalities (green lines) but in different positions characterized by the angle γ between the border (x-axis) and the centroid of the area (orange line). Panel **C** shows the value of the classic niche difference as a function of γ. Note that in the structural approach, the structural analog of niche difference (Ω) does not change as a function of γ. The dashed lines correspond to the values of γ shown in Panels **A** and **B**. The red line in Panel **C** corresponds to the renormalized structural analog of niche difference. Panels **D** and **E** show different areas (Ω), where the bottom slope lies on the border (x-axis). Panel **F** shows the value of these areas calculated as the niche difference under the structural approach (x-axis) and the classic niche difference (y-axis). Note that the classic niche difference is always 1. The dashed lines correspond to the values of Ω shown in Panels **D** and **E**.

As explained in the main text, simple inequalities equivalent to the MCT's ones for n-species do not exist. Therefore, there is no straightforward way to incorporate the competitive imbalance in the structural approach. Note that in the two species case, incorporating the competitive imbalance is equivalent to renormalizing the intrinsic growth rates of the two species by $r_1 \to r_1/\sqrt{\alpha_{11}\alpha_{12}}$ and by $r_2 \to r_2/\sqrt{\alpha_{21}\alpha_{22}}$. Then we also need to renormalize the interaction strengths as follows

$$\begin{bmatrix} \alpha_{11} & \alpha_{12} \\ \alpha_{21} & \alpha_{22} \end{bmatrix} \longrightarrow \begin{bmatrix} \alpha_{11}/\sqrt{\alpha_{11}\alpha_{12}} & \alpha_{12}/\sqrt{\alpha_{11}\alpha_{12}} \\ \alpha_{21}/\sqrt{\alpha_{21}\alpha_{22}} & \alpha_{22}/\sqrt{\alpha_{21}\alpha_{22}} \end{bmatrix}.$$

Finally, we can recompute the solid angle with the renormalized interaction strengths. For two species, the renormalized solid angle behaves in a similar way as the classical niche difference (shown by the red line on Figure S1.C). More generally, in dimension n, we may renormalize the interaction strengths as follows

$$\alpha_{ij} \longrightarrow \frac{\alpha_{ij}}{\sqrt[n]{\prod_{k=1}^{n} \alpha_{ik}}}$$

and compute the solid angle (Ω) based on the renormalized interaction strength. However, this renormalization as in MCT's approach is informative if no interspecific interaction is close to zero (see discussion above). Moreover, the comparison of niche differences (at any n-dimensional side in the simplex, is only possible under a structural approach. Under MCT's framework, as we would require to re-scale the matrix of competition coefficients for each pairwise case (or n-dimensional side in the simplex), each niche difference would lead to different units (defined by the particular re-scaling), making impossible their straight comparison across matrices or dimensions. In fact, to make all niche differences with the same units, one would need to remove the re-scaling, going back to the structural approach.

Appendix S6: Mathematical derivation and numerical estimation of the structural analog of niche difference Ω

The structural analog of niche difference is mathematically defined as the normalized solid angle of the cone defining the feasibility domain. We recall that this cone is generated by the column-vectors of the interaction strength matrix:

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

where

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

The solid angle of such a cone can be computed by the following multiple integration (for the mathematical derivation and details see Ribando, 2006):

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

The solid angle has been normalized such that $\Omega = 1$ in absence of interspecific interaction ($\alpha_{ij} = 0, i \neq j$). Moreover, by setting $\boldsymbol{\alpha}^T \boldsymbol{\alpha} = \frac{1}{2}\Sigma^{-1}$, the above integration transforms into:

$$\Omega = \frac{2^n}{(2\pi)^{n/2} \sqrt{|\det(\Sigma)|}} \int \cdots \int_{\boldsymbol{R}^n_{\geq 0}} e^{-\boldsymbol{x}^T \frac{1}{2} \Sigma^{-1} \boldsymbol{x}} d\boldsymbol{x},$$

which is (up to a multiplicative factor of 2^n) the cumulative distribution of a multivariate normal distribution centered in zero and of variance-covariance Σ. The cumulative distribution of a multivariate normal distribution can efficiently be estimated using the quasi Monte-Carlo algorithm developed by A. Genz (Genz and Bretz, 2009; Genz et al., 2016).

References

Genz, A., and F. Bretz. 2009. Computation of Multivariate Normal and t Probabilities. Lecture Notes in Statistics, Vol. 195. Springer-Verlage, Heidelberg.

Genz, A., F. Bretz, T. Miwa, X. Mi, F. Leisch, F. Scheipl, and T. Hothorn, 2016. mvtnorm: Multivariate Normal and t Distributions. R package version 1.0-5. R

Foundation for Statistical Computing. URL
`http://CRAN.R-project.org/package=mvtnorm`.

Ribando, M. J. 2006. Measuring Solid Angles Beyond Dimension Three. Discrete & Computational Geometry **36**:479–487.

Appendix S7: Geometric shapes of the feasibility domain

Here, we explore the different geometric shapes of the feasibility domain and their effect on multispecies coexistence. To do this, we randomly generated 20 thousand globally stable communities with different number of species, where the interaction matrices were drawn following a niche framework (see below). For each generated community, its structural analog of niche difference Ω was calculated, and then different vectors of intrinsic growth rates $\boldsymbol{r}$ were sampled and used to compute the number of coexisting species and the structural analog of fitness difference θ. The number of coexisting species was computed by solving the abundances at equilibrium N_i^* (abundances greater than zero are considered as coexisting species). The structural analog of fitness difference was computed by comparing the sampled vector $\boldsymbol{r}$ and the corresponding centroid of the feasibility domain $\boldsymbol{r}_c$.

We find that for communities with more than 2 species, there is no longer the clear division between regions of coexistence and exclusion, as in the 2-species case (Fig. S1). While the combination of high structural analog of niche differences and low structural analog of fitness differences yield higher chances of coexistence as in the 2-species case, now communities with the same combination of structural analog of niche and fitness differences can have a different number of coexisting species. These findings reveal that, in contrast to the 2-species case, multispecies coexistence cannot be predicted with niche and fitness differences only. The reason is that two multispecies communities with the same structural analog of niche difference may not tolerate the same structural analog of fitness difference. This happens because various geometric shapes of the feasibility domain (defined by the pairwise interactions) can produce the same structural analog of niche difference Ω (Figs. S2A and S2B). This variable geometry implies that a community can tolerate a greater structural analog of fitness difference in some directions than others.

The above limitations reveal a challenge when defining the structural analog of niche difference in systems with more than two competitors, and this involves taking into account the shape of the feasibility domain. Unfortunately this is not an easy task, but one possible solution involves computing the asymmetry of the feasibility domain. This asymmetry can be estimated by the variation among all the n-faces of the given multidimensional cone. This can be computed by the variance of all the n-structural analog of niche differences generated by removing each of the n-species in the community independently. For instance, if we have a 3-species system, the feasibility domain will form a 3-dimensional cone and can be projected on the 2-dimensional simplex. The projection corresponds to a triangle, and each of its sides corresponds to the length of the feasibility domain of each pairwise interaction. If the pairwise interactions are symmetric and equal, this variance would be zero. The higher the variance is, the higher the asymmetry of the feasibility domain.

Figure S2C shows that for distinct 3-species communities with the same structural analog of niche difference, the higher the variance or asymmetry in their feasibility domain, the lower their minimum structural analog of fitness difference that can be tolerated in any particular direction. Note that while the minimum structural analog of fitness difference is a good indicator of the level of tolerance under random perturbations, the natural variation in intrinsic growth rates may tend to fall in one particular direction. Thus, systems with high asymmetry do not need to be vulnerable systems necessarily.

Niche framework

We generated 10 thousand random matrices following a niche overlap framework (MacArthur and Levins, 1967; Levins, 1968). These matrices are by definition globally stable, requiring only to have feasible equilibrium points to fulfill our conditions of species coexistence. Specifically, these matrices were generated using the following procedure. For a matrix of dimension S, assuming a one dimensional niche space, the diet of species i is described by the niche utilization function. These functions are usually taken as a Gaussian-like curve:

$$g_i(x) = \frac{a_i}{\sqrt{2\pi}\sigma_i} e^{-\frac{x-\mu_i}{2\sigma_i^2}},$$

where σ_i is the niche width of species i, a_i is the amplitude, and μ_i the diet center. Then the competition coefficients are calculated as

$$\alpha_{ij} = \int g_i(x) g_j(x) dx.$$

Therefore, we can write

$$\alpha_{ij} = \frac{a_i a_j}{\sqrt{\sigma_i^2 + \sigma_j^2}} e^{-\frac{1}{2}\frac{(\mu_i-\mu_j)^2}{(\sigma_i^2+\sigma_j^2)}}.$$

Note that the matrix $\boldsymbol{\alpha}$ is in general not symmetric, unless we assume the same niche width and niche amplitude for all species. Recall that these interaction matrices are by definition positive definite thus Volterra-dissipative, and therefore, a feasible equilibrium point is globally stable (MacArthur and Levins, 1967; Svirezhev and Logofet, 1983; Logofet, 1993).

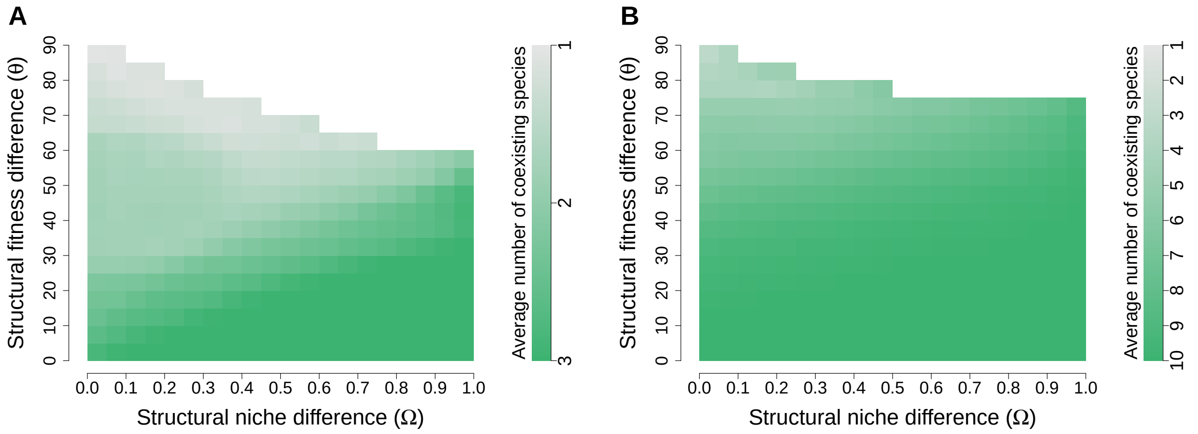

Figure S1: **Structural analog of niche and fitness differences for n-species communities.** Panel **A** and **B** show, respectively, the average number of coexisting species in (globally stable) randomly generated communities of 3 and 10 species as a function of structural analog of niche (Ω) and fitness differences (θ). The darker (greener) the region, the more the expected number of species that can coexist with a given combination of structural analog of niche and fitness differences. Higher structural analog of fitness differences can be computed in combination with lower structural analog of niche differences because of geometric constraints, and must not be interpreted as if lower structural analog of niche differences can tolerate higher structural analog of fitness differences.

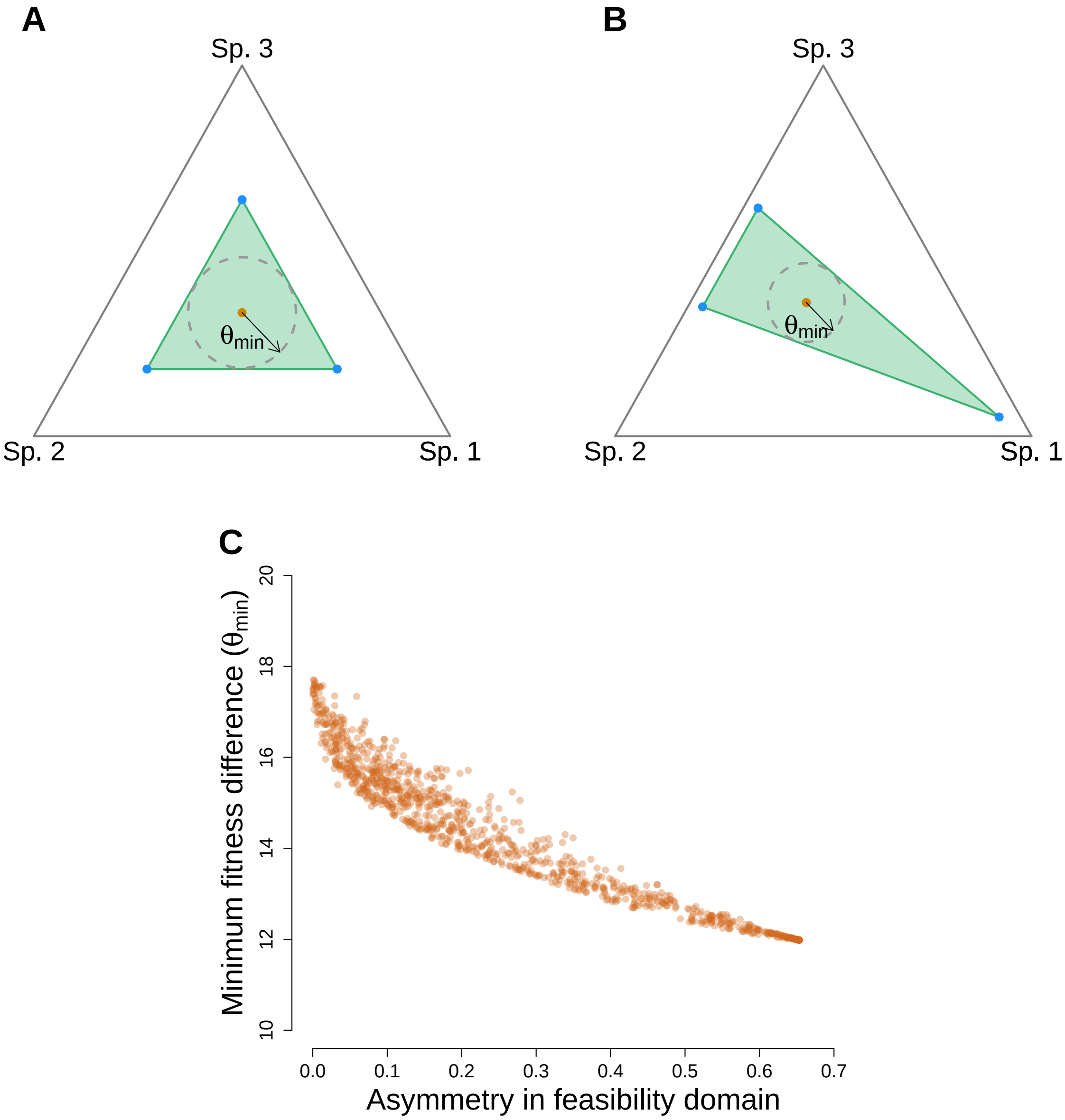

Figure S2: **Structural analog of niche, fitness, and asymmetry.** Panels **A** and **B** show the projected feasibility domain of two distinct communities with 3 species. Both communities have the same structural analog of niche difference (green area of feasibility domain), but different geometric shapes (defined by their pairwise interactions). The black vectors inside the feasibility domains correspond to the minimum structural analog of fitness difference (θ) that can be tolerated in any direction. Panel **C** shows the minimum tolerated structural analog of fitness difference as a function of the asymmetry in feasibility domain. Each point corresponds to a different 3-species community, all with the same structural analog of niche difference (Ω).

References

Levins, R. 1968. Evolution in Changing Environments: Some Theoretical Explorations. Princeton University Press, USA.

Logofet, D. O. 1993. Matrices and Graphs: Stability Problems in Mathematical Ecology. CRC Press.

MacArthur, R., and R. Levins. 1967. The Limiting Similarity, Convergence, and Divergence of Coexisting Species. Am Nat **101**:377–385.

Svirezhev, Y. M., and D. O. Logofet. 1983. Stability of Biological Communities. Mir Publishers.