

Abstract

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Many empirical studies motivated by an interest in stable coexistence have quantified negative density dependence, negative frequency dependence, or negative plant–soil feedback, but the links between these empirical results and ecological theory are not straightforward. Here, we relate these analyses to theoretical conditions for stabilisation and stable coexistence in classical competition models. By stabilisation, we mean an excess of intraspecific competition relative to interspecific competition that inherently slows or even prevents competitive exclusion. We show that most, though not all, tests demonstrating negative density dependence, negative frequency dependence, and negative plant–soil feedback constitute sufficient conditions for stabilisation of two-species interactions if applied to data for per capita population growth rates of pairs of species, but none are necessary or sufficient conditions for stable coexistence of two species. Potential inferences are even more limited when communities involve more than two species, and when performance is measured at a single life stage or vital rate. We then discuss two approaches that enable stronger tests for stable coexistence-invasibility experiments and model parameterisation. The model parameterisation approach can be applied to typical density-dependence, frequency-dependence, and plant–soil feedback data sets, and generally enables better links with mechanisms and greater insights, as demonstrated by recent studies.

Keywords

Coexistence, competition, conspecific effects, density-dependence, fitness differences, frequency-dependence, heterospecific effects, Lotka–Volterra, niche differences, plant, soil feedback, stabilisation.

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INTRODUCTION

Virtually every ecosystem contains multiple competing species that persist together for long periods of time. In some highly diverse tropical forests, hundreds of tree species co-occur within a single hectare, in diverse grasslands dozens of herb species within a square meter (Wilson *et al.* 2012). How such biodiversity is maintained is one of the central questions of ecology (Sutherland *et al.* 2013). This question is of both fundamental and applied interest, as answers to this question can help guide management efforts to conserve or restore biodiversity. Many studies therefore aim to understand the mechanisms contributing to the stable coexistence of species.

Stable coexistence is the long-term persistence of multiple competing species, with each species able to recover if perturbed to low density (e.g. Gotelli 1995; Chesson 2000; Begon *et al.* 2006; Chesson 2012) (See Box 1 for definition of terms given in italics). It has long been recognised that stable coexistence requires that intraspecific competition be sufficiently

greater than interspecific competition (Chesson 2000). Many theoretical studies have determined the mathematical conditions for stable coexistence in different models – e.g. relationships among competition coefficients in the Lotka–Volterra equations, limiting similarity in niche models, etc. (e.g. Tilman 1982; Chesson 2000; Chase & Leibold 2003; Saavedra *et al.* 2017; Germain *et al.* 2018). And many empirical studies in plant communities have sought to quantify the negative effects of the presence, density, or frequency of *conspecifics* on performance (e.g. Wills *et al.* 1997; Webb & Peart 1999; Klinironomos 2002; Harpole & Suding 2007; Petermann *et al.* 2008; Comita *et al.* 2010; Metz *et al.* 2010; LaManna *et al.* 2017, Zhu *et al.* 2018).

Most of these empirical studies fall into one of three categories: *density-dependence studies*, *frequency-dependence studies*, and *plant–soil feedback studies*. Density-dependence studies examine how growth, survival, reproduction, or population growth rate of a species vary with the density of conspecifics and sometimes also with the density of heterospecifics

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Box 1. Concepts and definitions

Stable coexistence is the long-term persistence of multiple competing species, without any species being competitively excluded by the others, and with each species able to recover from perturbation to low density.

Modern coexistence theory

Modern coexistence theory describes the conditions leading to stable coexistence in terms of stabilisation due to niche differences being sufficiently strong to prevent competitive exclusion due to “fitness differences”. It is grounded in work by Chesson (Chesson 2000; Chesson & Kuang 2008; Chesson 2012, 2018).

Stabilisation *sensu* Chesson is an excess of intraspecific competition relative to interspecific competition; it inherently slows or even prevents competitive exclusion and is a necessary but not sufficient condition for stable coexistence. Mathematically, the condition for stabilisation is equivalent to the condition for local stability of the multi-species equilibrium; this is not sufficient for stable coexistence because it does not guarantee that this equilibrium is *feasible*.

Niche differences between species are differences in limiting factors, which can relate to limitation by resources and/or by natural enemies. Niche differences result in stabilisation.

Fitness differences between species are differences in competitive ability (Hart *et al.* 2018). In the absence of niche differences, the species with the highest fitness will competitively exclude all other species. (Note that this use of “fitness” is different from its definition in evolutionary biology.)

Models and their analysis

The **invasion growth rate** of a species is its per capita population growth rate when it is rare and other species are at their equilibria in the absence of the focal species.

The **invasibility criterion** requires that each species have a positive invasion growth rate; it is a sufficient condition for stable coexistence in two-species communities (Maynard-Smith 1982; Chesson 2000, 2018).

An **equilibrium point** in a model of interacting species is a combination of densities at which all species have population growth rates of zero. An equilibrium point is **feasible** if all species have positive densities at this point (as in Barabas *et al.* 2016); it is **locally stable** if species’ densities tend to return to this point when perturbed away from it, and it is **globally stable** if species densities approach this point for any combination of starting densities.

A **necessary** condition is a condition that must be true for an activity or event to take place. (For example, participating in an Olympic event is a necessary condition to win an Olympic medal, but not a sufficient condition as only the top finishers receive medals.)

A **sufficient** condition is a condition that, if true, guarantees that an activity or event takes place, but the activity or event may still take place if the condition is not satisfied. (For example, winning an Olympic event is a sufficient condition for receiving a medal, but not a necessary condition as medals are also awarded for second and third place.)

Empirical studies

A **density-dependence study** relates the performance of individuals or populations of one or more species to conspecific density, and sometimes also to heterospecific density.

A **frequency-dependence study** relates the performance of individuals or populations of one or more species to conspecific frequency, the density of conspecifics divided by total density of conspecifics and heterospecifics.

A **plant-soil feedback study** evaluates the performance of one or more plant species in soils conditioned by conspecifics and in soils conditioned by heterospecifics, or in monocultures of conspecifics and heterospecifics.

A **model-parameterisation study** estimates the parameters of a species interaction model (e.g. the Lotka–Volterra competition model) from empirical data on how the performance of individuals or populations varies with the density of conspecifics and of one or more competing species.

By **performance** we mean per capita population growth rate or a vital rate that contributes to it, such as individual survival, growth and recruitment.

A **conspecific** is an individual of the same species.

A **heterospecific** is an individual of a different species.

(e.g. Webb & Peart 1999; Harms *et al.* 2000; HilleRisLambers *et al.* 2002; Comita *et al.* 2010). Frequency-dependence studies are similar, but focus on how performance is related to conspecific frequency, that is, the density of conspecifics divided by the total density summed over all species (Harpole & Suding 2007). Plant–soil feedback studies compare species performance in soils cultured by conspecifics vs. heterospecifics, or in monocultures of conspecifics vs. heterospecifics (e.g.

Klironomos 2002; Petermann *et al.* 2008; McCarthy-Neumann & Kobe 2010a,2010b; Yamazaki *et al.* 2009; Alvarez-Loayza & Terborgh 2011). We ourselves have conducted various such studies (e.g. Harms *et al.* 2000; Comita *et al.* 2010). Unfortunately, as previously noted by Siepelski & McPeek (2010) and Adler *et al.* (2018), among others, many of these studies do not provide the information needed to fully assess conditions for stable coexistence. But what do they tell us, exactly? The

linkages between what we measure in empirical studies and the equations in theoretical studies are not transparent.

Our goal is to clarify the relationships of these different types of studies to conditions for stabilisation and stable coexistence. We start by reviewing the mathematical conditions for stable coexistence under the two-species Lotka–Volterra competition model, a simple model that serves to illustrate the relevant general principles. We specifically address conditions for *stabilisation*, defined as an excess of intraspecific competition relative to interspecific competition that inherently slows or even prevents competitive exclusion, as well as the more stringent conditions for stable coexistence. Next, we explore the implicit mathematical conditions evaluated in the three categories of empirical studies distinguished above, and relate them to theoretical conditions for stabilisation and stable coexistence in classical two-species competition models that have been used in the elaboration of modern coexistence theory (Chesson 2000, 2012, 2018). We conclude that most (but not all) of these types of studies can provide evidence for stabilisation of two-species interactions if applied to data on per capita population growth rates of two species, and that none can provide evidence for stable coexistence. We further evaluate what such studies can tell us (if anything) about coexistence in multi-species communities, or when measurements involve a single life stage or vital rate rather than per capita population growth rates, or when studies otherwise deviate from model assumptions. We then discuss two approaches that can enable strong tests of stable coexistence–invasibility experiments and model parameterisation studies — and their challenges and limitations. The model parameterisation approach can in many cases be applied to the types of data collected in studies of density-dependence, frequency-dependence, and plant–soil feedback, potentially enabling stronger tests of stabilisation and stable coexistence with the same data sets. Throughout, we focus on plant communities, though our results are also applicable to other types of organisms.

THEORETICAL CONDITIONS FOR STABILISATION AND STABLE COEXISTENCE

We begin by deriving the mathematical conditions for stabilisation and stable coexistence in the Lotka–Volterra model for two competing species, under the parameterisation used by Chesson (2000, 2012, 2018) in his elaboration of *modern coexistence theory*. Here competition can include not only direct negative effects due to resource competition but also indirect negative effects due to interactions with natural enemies (i.e. apparent competition, Chesson & Kuang 2008; Chesson 2018). If N_1 and N_2 are the abundances of species 1 and 2, respectively, this model can be written as

$$\frac{1}{N_1} \frac{dN_1}{dt} = r_1(1 - \alpha_{11}N_1 - \alpha_{12}N_2) \quad (1a)$$

$$\frac{1}{N_2} \frac{dN_2}{dt} = r_2(1 - \alpha_{21}N_1 - \alpha_{22}N_2) \quad (1b)$$

Equation (1) describes how the per capita growth rate of each species (left hand side) is reduced below its intrinsic rate of increase (r_1, r_2) by intraspecific (α_{11}, α_{22}) and interspecific (α_{12}, α_{21}) competition. In this parameterisation, the α 's are the absolute competition coefficients, i.e. the per capita

competitive effect of conspecific and heterospecific individuals on the per capita growth rate of a given species. Eqn 1 is an alternative parameterisation (Chesson & Huntley 1997; Chesson 2000, 2012, 2018) of the original equations from Lotka (1920) and Volterra (1928). The intraspecific competition coefficients in these equations, α_{11} and α_{22} , are equivalent to the inverse of the carrying capacities, K_1 and K_2 , in the original equations ($\alpha_{11} = \frac{1}{K_1}, \alpha_{22} = \frac{1}{K_2}$) and the interspecific competition coefficients are rescaled accordingly ($\alpha_{12} = \frac{\alpha'_{12}}{K_1}, \alpha_{21} = \frac{\alpha'_{21}}{K_2}$).

Two species can coexist stably if each species is able to invade a monoculture of the other species, thus satisfying the *invasibility criterion* (Box 1; e.g. Chesson 1994, 2000). Given equations for the per capita population growth rate such as eqn 1, this criterion can be evaluated by setting the density of one of the species to zero and the other species to its monospecific carrying capacity (e.g. $N_1 = 0, N_2 = K_2 = \frac{1}{\alpha_{22}}$). The per capita growth rate of the species at zero abundance is its *invasion growth rate*, \bar{r}_i . For the Lotka–Volterra competition model (eqn 1), the invasion growth rates are

$$\bar{r}_1 = r_1 \left(1 - \frac{\alpha_{12}}{\alpha_{22}}\right) \quad (2a)$$

$$\bar{r}_2 = r_2 \left(1 - \frac{\alpha_{21}}{\alpha_{11}}\right) \quad (2b)$$

The invasibility criterion requires that these are both greater than zero (i.e. $\bar{r}_1 > 0$ and $\bar{r}_2 > 0$), which implies

$$\alpha_{11} > \alpha_{21} \quad (3a)$$

and

$$\alpha_{22} > \alpha_{12} \quad (3b)$$

Together, these are necessary and sufficient conditions for stable coexistence in the two-species Lotka–Volterra competition model (eqn 1). These conditions can also be derived from comparisons of *fitness differences* with *niche differences* using the methods of modern coexistence theory (see Box 2). For this model (but not all models), stable coexistence occurs if and only if there is a globally stable, feasible equilibrium point (see Box 1 for definitions and textbooks such as Gotelli 1995 for a longer treatment).

It is often correctly stated that coexistence requires intraspecific competition to be stronger than interspecific competition – but this statement is imprecise with respect to the exact comparisons to be made (see also Adler *et al.* 2018). More precisely, as shown in eqn 3a,b, stable coexistence requires that each species must have a more negative effect *on* itself than *on* the other (i.e. $\alpha_{11} > \alpha_{21}$ and $\alpha_{22} > \alpha_{12}$; see Box 3 for an explanation of our terminology of effects *of* and *on* species). Importantly, stable coexistence is not assured if each species is more suppressed by an individual *of* its own species than by an individual *of* the other species (i.e. $\alpha_{11} > \alpha_{12}$ and $\alpha_{22} > \alpha_{21}$). Larger effects *of* focal conspecifics than *of* the competing species can be consistent with either stable coexistence or competitive exclusion. For example, these conditions are met in both Fig. 1a and b, but there is stable coexistence only in Fig. 1a (see figure caption for details).

Stable coexistence requires stabilisation, an excess of intraspecific effects relative to interspecific effects that

Box 2. Niche differences and fitness differences in modern coexistence theory

In modern coexistence theory, niche differences between two species are assessed by evaluating the degree to which their niche overlap, denoted ρ , is less than one. If ρ is equal to one, there is complete niche overlap and thus no niche difference; if ρ is less than one, niche overlap is incomplete, meaning there is a niche difference and thus stabilisation. For the Lotka–Volterra competition model, niche overlap is calculated as

$$\rho = \sqrt{\frac{\alpha_{21}\alpha_{12}}{\alpha_{11}\alpha_{22}}} \quad (5)$$

(e.g. Chesson 2012, 2018). We can interpret this equation to mean that lower niche overlap is associated with lower interspecific competition relative to intraspecific competition. Note that the condition $\rho < 1$ is equivalent to the inequality of eqn 4.

Fitness differences *sensu* Chesson between two species are assessed by evaluating the deviation of the ratio of the two species' fitnesses from 1. (This use of the term "fitness" is distinct from its definition in evolutionary biology.) That is, given individual fitnesses k_1 and k_2 of species 1 and 2, their fitness difference is quantified using the fitness ratio $\frac{k_1}{k_2}$. If the fitness ratio is equal to 1, the two species have equal fitness, and thus there is no fitness difference. A fitness ratio $\frac{k_1}{k_2}$ greater than 1 indicates that species 1 has higher fitness and will win in competition absent of sufficient niche differences, with greater values of the ratio indicating greater fitness differences. A fitness ratio $\frac{k_1}{k_2}$ less than 1 indicates that species 2 has higher fitness, with lower values of the ratio indicating greater fitness differences. For the Lotka–Volterra competition model, the fitness ratio between two species is calculated as

$$\frac{k_1}{k_2} = \sqrt{\frac{\alpha_{22}\alpha_{21}}{\alpha_{11}\alpha_{12}}} \quad (6)$$

(e.g. Chu & Adler 2015; Chesson 2018). We can interpret this equation to mean that species 1 has a higher fitness than species 2 if the product of the competitive effects on 1 is smaller than the product of the competitive effects on 2.

Stable coexistence occurs when niche differences are large enough to overcome fitness differences. Mathematically, this can be written as the following general conditions:

$$\frac{1}{\rho} > \frac{k_1}{k_2} \quad (7a)$$

and

$$\frac{1}{\rho} > \frac{k_2}{k_1} \quad (7b)$$

or equivalently

$$\rho < \frac{k_1}{k_2} < \frac{1}{\rho} \quad (7c)$$

(e.g. Chesson 2000; Chesson & Kuang 2008; Chesson 2018). Substituting eqns 5 and 6 into eqn 7 leads to the same conditions for stable coexistence as in eqn 3.

We can interpret differences among the various Lotka–Volterra competition scenarios shown in Fig. 1 in terms of whether they satisfy these inequalities (Table 1). The scenarios in Fig. 1a and b both feature stabilisation ($\frac{1}{\rho} > 1$, equivalently $\alpha_{22}\alpha_{11} > \alpha_{12}\alpha_{21}$); the associated niche difference is greater than the fitness difference in Fig. 1a, thus insuring stable coexistence, but not in Fig. 1b. In the scenarios of Fig. 1c and d, there is no niche difference and no stabilisation.

Graphically, we can understand the stabilisation condition in terms of differences in the slopes of the isoclines. Stabilisation is present if and only if the two-species equilibrium point is locally stable (Fig. 1a and b) rather than unstable (Fig. 1c), which requires that the two isoclines cross in the "right" way. In particular, this point is locally stable if the slope of the isocline of species 1 is more negative than the slope of the isocline of species 2. The slopes of the isoclines of species 1 and 2 are $-\frac{\alpha_{11}}{\alpha_{12}}$ and $-\frac{\alpha_{21}}{\alpha_{22}}$, respectively, and this requirement thus is equivalent to the condition for stabilisation (eqn 4, see Appendix S1). Because stabilisation is present in Fig. 1b, this scenario could be made into one of stable coexistence simply by increasing the fitness of species 1 or decreasing the fitness of species 2 sufficiently to move the two-species equilibrium point to an area where both species have positive densities (i.e. to make the equilibrium feasible). In contrast, changing the fitness of either species in the scenario of Fig. 1d would at best move the system to alternative stable states (Fig. 1c), because there is no stabilisation (the two-species equilibrium is unstable).

inherently slows or prevents competitive exclusion (Box 1). Fundamentally, stabilisation is the signature of niche differences, differences among species in their limiting factors and

thus in their niches (e.g. in their resources used and/or in their natural enemies). In general, the condition for stabilisation is equivalent to that for local stability of the multi-species

equilibrium; it does not guarantee that the equilibrium is feasible (i.e. positive abundances of all species, Box 1). For the Lotka–Volterra model, the condition for stabilisation is

$$\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21} \quad (4)$$

(see Appendix S1 in Supporting Information and Box 2 for derivations). Stabilisation therefore requires the total of intraspecific effects to be stronger than the total of interspecific effects, whereas stable coexistence further requires each species to have a stronger effect *on* itself than *on* its competitor. In the language of modern coexistence theory, stabilisation indicates that there are niche differences, whereas stable coexistence further requires these niche differences to be greater than the fitness differences (see box 2). Stabilisation is thus a necessary, but not sufficient condition for stable coexistence. It is not sufficient in and of itself because stabilisation may be too weak relative to fitness differences, such that it merely slows but does not prevent competitive exclusion. Competitive exclusion despite stabilisation means the multi-species equilibrium point is infeasible, even though it is stable. Thus, for example, Fig. 1a and b both feature stabilisation (stable equilibria), but only Fig. 1a features stable coexistence (a feasible, stable equilibrium), whereas Fig. 1c and d both show scenarios lacking stabilisation (unstable equilibria).

An empirical example can illustrate how stronger intraspecific than interspecific effects can arise in practice, how these effects should be compared and how they may or may not be sufficient for stable coexistence. Consider competition between a shallow-rooted plant species (species 1) and a deep-rooted species (species 2). Because individuals of the deep-rooted species obtain water and nutrients from the same depth, we expect that a focal individual of the deep-rooted species will have stronger competitive effects *on* conspecific individuals than *on* heterospecific individuals (i.e. $\alpha_{22} > \alpha_{12}$). Consequently, when the deep-rooted species is at its carrying capacity, individuals of the shallow-rooted species will be less suppressed than individuals of the deep-rooted species, and the shallow-rooted species will have a positive invasion growth rate (eqn 2b). If individuals of the shallow-rooted species also have stronger competitive effects *on* conspecifics than *on* heterospecifics (i.e. $\alpha_{11} > \alpha_{21}$), then the deep-rooted species will also have a positive invasion growth rate, and the two species will stably coexist (e.g. Fig. 1a). However, if the shallow-rooted species strongly affects the deep-rooted species by preventing leaching of nutrients and water to lower layers, then it is possible that the shallow-rooted species might actually have a larger effect *on* the deep-rooted species than *on* itself (i.e. $\alpha_{11} > \alpha_{21}$), violating eqn 3a and making it impossible for the deep-rooted species to invade a community of the shallow-rooted species. If this is the case and the deep-rooted species still has a larger effect *on* itself than *on* the shallow-rooted species ($\alpha_{22} > \alpha_{12}$), then the shallow-rooted species will competitively exclude the deep-rooted species, and there will be no stable coexistence, even though there may be stabilisation (Fig. 1b).

LINKING COMMON EMPIRICAL ANALYSES TO THEORY

Many studies of density-dependence, frequency-dependence, and plant-soil feedback have quantified measures of

conspecific and/or heterospecific effects. In this section, we detail the exact mathematical conditions under the two-species Lotka–Volterra competition model corresponding to each of the types of analyses commonly conducted in such studies (Table 1, with derivations in Appendix S2). We compare these tested conditions with the conditions for stabilisation and stable coexistence defined by modern coexistence theory for simple two-species Lotka–Volterra competition models. For readers that may be more familiar with alternative parameterisations of the Lotka–Volterra model, we provide equivalent conditions for other common parameterisations (Tables S1, S2). We also provide conditions for the Beverton–Holt model (Beverton & Holt 1957), which lead to qualitatively similar linkages with empirical findings (Tables S3 and S4).

If the conditions measured in empirical studies do not correspond with the relevant theoretical conditions for stabilisation or stable coexistence, we conclude that the studies necessarily provide limited insight into stabilisation and stable coexistence. If the empirically measured conditions do correspond, the studies may or may not provide good evidence for stabilisation or stable coexistence. Such conclusions further depend on whether the empirical measures of performance are good proxies for per capita population growth rates, whether the two-species criteria are relevant for the study system and design, and whether the model adequately describes the study system (see Critical assumptions and limitations of these linkages). Moreover, these conclusions are contingent upon statistical analyses producing unbiased estimates of the quantities of interest, a problem we do not address here (Freckleton *et al.* 2006; Dickie *et al.* 2012).

We recognise that many of the cited studies were not originally intended to assess stabilisation or stable coexistence, and that such studies should not be judged based on their success or failure in doing so. Nonetheless, we consider it useful to evaluate how these analyses (including our own) relate to the theoretical conditions for stabilisation and stable coexistence.

Density-dependence studies

Studies of negative density dependence commonly report regression coefficients relating performance of the focal species to density of conspecifics and/or heterospecifics. We say such coefficients quantify “per capita” effects, in the sense that the total effect on the performance of the focal species is the product of the estimated coefficients and the densities of individuals.

A number of studies investigate only how performance is related to conspecific density, without making any comparison with heterospecific effects (study type 1A in Table 1). For example, Harms *et al.* (2000) analysed how seedling emergence of tropical plant species varied with the densities of conspecific seeds arriving nearby, and concluded that there was negative density-dependence in all 53 focal species. What does such a finding of conspecific negative density-dependence in multiple species in and of itself tell us about stabilisation and species coexistence? Assume for the moment that the performance measure (here seedling emergence) is a good proxy for per capita population growth rate (an issue discussed further in Critical assumptions and limitations of these linkages), and

that density-dependence is estimated without bias. In the Lotka–Volterra competition model, a finding of negative density-dependence of per capita population growth for species 1 indicates that $\alpha_{11}r_1 > 0$, and because the intrinsic rate of increase is necessarily positive ($r_1 > 0$), this in turn implies $\alpha_{11} > 0$. In a competition model, this is a necessary condition for stabilisation and stable coexistence. However, even if conspecific effects are quantified in two species ($1 \rightarrow 1$, i.e. the effects of species 1 on species 1, and $2 \rightarrow 2$), with both showing negative conspecific density-dependence (thus establishing $\alpha_{11} > 0$ and $\alpha_{22} > 0$), this does not constitute a sufficient condition for stabilisation much less for stable coexistence of this pair of species. Stable coexistence requires mutual

invasibility of both species, and quantification of intraspecific effects alone reveals nothing of each species' performance in a community of its competitor. Establishing stabilisation or stable coexistence requires appropriate comparisons of intraspecific and interspecific effects ($\alpha_{22}\alpha_{11} > \alpha_{12}\alpha_{21}$ for stabilisation; $\alpha_{11} > \alpha_{21}$ and $\alpha_{22} > \alpha_{12}$ for stable coexistence). (See appendix S2, section 2.1.2 for mathematical details.)

Even findings that conspecific negative density dependence is overcompensating do not in and of themselves indicate stabilisation or stable coexistence, in the absence of comparisons with heterospecific effects. Overcompensating negative density dependence occurs when (per capita) performance decreases more than proportionally with increasing density (Freckleton

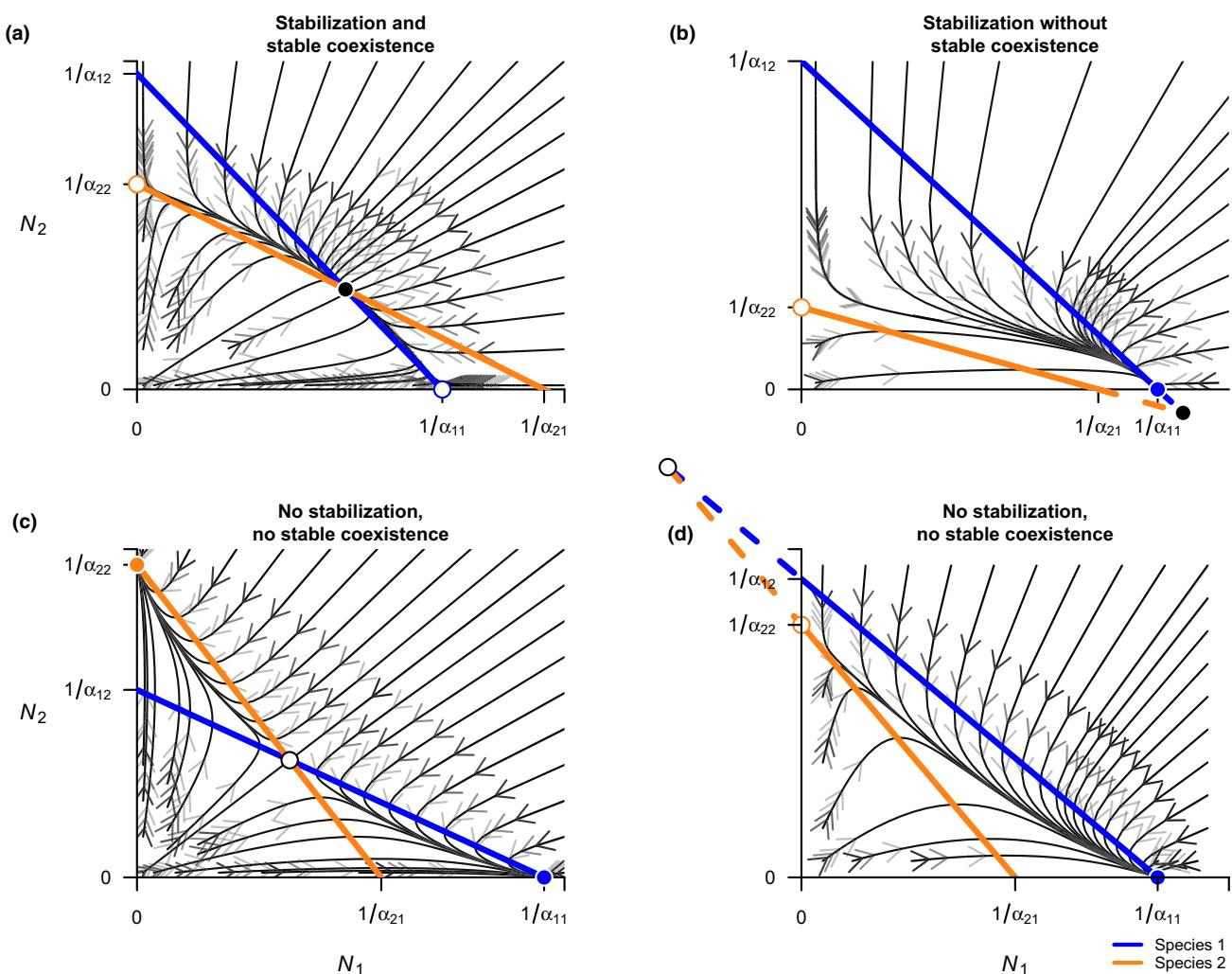


Figure 1 Phase planes for the two-species Lotka–Volterra competition model under four different scenarios. These phase planes, also known as state-space graphs (Gotelli 1995) show how growth rates of the two populations vary with the densities of the two species, with arrows indicating the direction of change in abundances (grey arrows). The zero net growth isoclines of species 1 and 2 (blue and orange lines, respectively) indicate combinations of species densities at which the population growth rate of species 1 and 2, respectively, are zero (dashed lines indicate isoclines outside the feasible domain). Circles indicate equilibrium points at which the growth rates of both species are zero, with filled circles indicating stable equilibrium points (to which populations return if perturbed) and open circles indicating unstable equilibrium points. Grey arrows indicate the direction of change in densities and thus the population growth rates of the two species at different combinations of densities. The point where the isoclines cross is shown in all panels, even those where it is not attainable (b, d, due to negative population densities) because it is relevant to understanding the meaning of stabilisation (see Box 2). The parameter values ($r_1, r_2, \alpha_{11}, \alpha_{21}, \alpha_{22}, \alpha_{12}$) for panel A are (0.25, 0.25, 0.02, 0.015, 0.02, 0.013), for B are (0.5, 0.25, 0.04, 0.048, 0.08, 0.02), for C are (0.25, 0.25, 0.015, 0.025, 0.015, 0.025), and for D are (0.25, 0.25, 0.012, 0.02, 0.013, 0.011). Additional parameters for making the graphs and the full R code are given in Appendix S4.

Table 1 Types of empirical studies of density-dependence, frequency-dependence, and plant-soil feedback classified by their design and the tests performed, along with their equivalent mathematical conditions under the two-species Lotka–Volterra competition model, the relevance of the test for evaluating stabilisation and stable coexistence in the Lotka–Volterra model, and examples of studies performing such analyses (not an exhaustive list)

General study design	Study type	What do the analyses test?	Equivalent test under the 2-species Lotka–Volterra competition model (eqn 1)	Relevance to stabilisation (eqn 4)	Relevance for stable coexistence (eq. 3)	Examples of studies
Density-dependence studies	1A	Per capita effects of conspecifics are negative	$r_1\alpha_{11} > 0$ AND $r_2\alpha_{22} > 0$ (see SI2.1.1)	Necessary , but not sufficient (comparison with heterospecifics is missing)	Necessary , but not sufficient (comparison with heterospecifics is missing)	Wills <i>et al.</i> (1997), Webb & Peart (1999), Harms <i>et al.</i> (2000), Packer & Clay (2000), Blundell & Peart (2004), Bagchi <i>et al.</i> (2010), Bagchi <i>et al.</i> (2014), Johnson <i>et al.</i> (2014), Zhu <i>et al.</i> (2018)
	1B	Per capita effects of conspecifics are more negative than per capita effects of heterospecifics	$r_1\alpha_{11} > r_1\alpha_{12}$ AND $r_2\alpha_{22} > r_2\alpha_{21}$ (see SI2.1.2)	Sufficient Not necessary*	Not necessary or sufficient (incorrect comparison of competition coefficients)	Connell <i>et al.</i> (1984); HilleRisLambers <i>et al.</i> (2002), Peters (2003), Webb <i>et al.</i> (2006), Comita <i>et al.</i> (2010), Metz <i>et al.</i> (2010), Kobe & Vriesendorp (2011), Johnson <i>et al.</i> (2012), LaManna <i>et al.</i> (2017), Ramage & Mangana (2017)
	1C	Per capita effects on conspecifics are more negative than per capita effects on heterospecifics	$r_1\alpha_{11} > r_2\alpha_{21}$ AND $r_2\alpha_{22} > r_1\alpha_{12}$ (see SI2.1.3)	Sufficient Not necessary* (confounding effects of r)	Not necessary or sufficient (confounding effects of r)	Ramage & Mangana (2017)
Frequency-dependence studies	2A	Negative frequency-dependence when total density is held constant at N_{tot}	$r_1(\alpha_{11} - \alpha_{12})N_{tot} > 0$ AND $r_2(\alpha_{22} - \alpha_{21})N_{tot} > 0$ (see SI2.2.1)	Sufficient Not necessary*	Not necessary or sufficient (incorrect comparison of competition coefficients)	Harpole & Suding (2007)
	2B	Negative frequency-dependence <i>sensu Adler <i>et al.</i> (2007)</i>	$\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$ (see SI2.2.2)	Necessary & Sufficient	Necessary Not sufficient [†]	None known
Plant-soil feedback studies	3A	Total effects of conspecifics are more negative than total effects of heterospecifics at arbitrary densities	$r_1(1 - \alpha_{11}N_1) < r_1(1 - \alpha_{12}N_2)$ AND $r_2(1 - \alpha_{22}N_2) < r_2(1 - \alpha_{21}N_1)$ (see SI 2.3.1)	Sufficient Not necessary*	Not necessary or sufficient (confounding effects of N)	Klironomos (2002), McCarthy-Neumann & Kobe (2010a, b), Petermann <i>et al.</i> (2008), Yamazaki <i>et al.</i> (2009)
	3B	Total effects on conspecifics are more negative than total effects on heterospecifics at arbitrary densities	$r_1(1 - \alpha_{11}N_1) < r_2(1 - \alpha_{21}N_1)$ AND $r_2(1 - \alpha_{22}N_2) < r_1(1 - \alpha_{12}N_2)$ (see SI2.3.2)	Not necessary or sufficient (confounding effects of r and N)	Not necessary or sufficient (confounding effects of r and N)	Alvarez-Llorente & Terborgh (2011)

*Even if one of these conditions is not satisfied, the condition for stabilisation ($\alpha_{22}\alpha_{11} > \alpha_{12}\alpha_{21}$) may still be met provided the other inequality is sufficiently unequal as to compensate such that the condition on the product of the inequalities still holds. See SI Appendix 2.

[†]If this condition is met and the population growth rate reaches zero at a frequency between zero and one, then these conditions in combination are sufficient for stable coexistence.

Box 3. Terminology of competitive effects *of* and *on* species

In two-species communities there are four different competitive effects, with four corresponding competition coefficients in the Lotka–Volterra competition model. We describe these four effects with the following terminology and symbols:

- α_{11} : Effect *of* species 1 *on* species 1 ($1 \rightarrow 1$)
- α_{12} : Effect *of* species 2 *on* species 1 ($2 \rightarrow 1$)
- α_{21} : Effect *of* species 1 *on* species 2 ($1 \rightarrow 2$)
- α_{22} : Effect *of* species 2 *on* species 2 ($2 \rightarrow 2$)

We thus refer to comparisons of α_{11} vs. α_{12} (or e.g. $r_1\alpha_{11}$ vs. $r_1\alpha_{12}$ in density-dependence studies, and more generally of $1 \rightarrow 1$ vs. $1 \rightarrow 2$) as comparisons of effects *on* conspecifics vs. heterospecifics. In contrast, we refer to comparisons of α_{11} vs. α_{21} (more generally $1 \rightarrow 1$ vs. $2 \rightarrow 1$) as comparisons of effects *of* conspecifics vs. heterospecifics. This is a critical distinction, as these are fundamentally different comparisons with different significance for species coexistence.

Some previous studies (e.g. Adler *et al.* 2018) refer to these as comparisons of competitive effects ($1 \rightarrow 1$ vs. $1 \rightarrow 2$) and competitive responses ($1 \rightarrow 1$ vs. $2 \rightarrow 1$), respectively. We do not adopt this terminology here because it is not fully consistent with previous usage of these terms. In the literature, the effect of species 1 on species 2 ($1 \rightarrow 2$) is said to depend on both the *competitive effect* of species 1 and the *competitive response* of species 2 (e.g. Goldberg 1990). For example, the effect of species 1 on species 2 may depend on the shade cast by species 1 (part of species 1's competitive effect), as well as the shade-tolerance of species 2 (part of species 2's competitive response). Referring to the comparison of the interactions $1 \rightarrow 1$ vs. $1 \rightarrow 2$ as a comparison of competitive effects on conspecifics vs. heterospecifics risks obscuring the fact that both interactions involve a competitive effect and a competitive response (and in fact, it is the responding species that differs between the two). Describing all interactions in terms of effects *of* a species *on* a species avoids this potential confusion.

& Lewis 2006; Mayfield & Stouffer 2017). The Lotka–Volterra competition model cannot accommodate overcompensating negative density dependence; however, the nonlinear Beverton–Holt model can and the conditions for stabilisation and stable coexistence still require comparisons of intraspecific and interspecific effects (Tables S3, S4). Biologically, we can understand this to mean that even if both species are strongly self-limiting, one may be a sufficiently stronger competitor that it prevents the invasion of the other.

Several studies further test whether per capita effects *of* conspecifics are more negative than per capita effects *of* heterospecifics (study type 1B in Table 1). For two species, this means comparing the effects of species 1 on itself ($1 \rightarrow 1$) with the effects of species 2 on species 1 ($2 \rightarrow 1$), and similarly comparing the effects of both species on species 2 ($2 \rightarrow 2$ vs. $1 \rightarrow 2$). Where more than two species are

involved, all heterospecifics may be lumped together, complicating interpretation, an issue we address later (see *Critical assumptions and limitations of these linkages*). For example, Comita *et al.* (2010) fitted seedling survival as a linear function of the densities of conspecific and of heterospecific neighbors, and compared conspecific and heterospecific regression coefficients. They found significant negative effects of conspecifics, but only weak effects of heterospecifics. In the two-species Lotka–Volterra competition system, demonstrating more negative per capita effects *of* conspecifics than *of* heterospecifics on per capita population growth in such a comparison of regression coefficients is equivalent to demonstrating $r_1\alpha_{11} > r_1\alpha_{12}$ and $r_2\alpha_{22} > r_2\alpha_{21}$, and thus $\alpha_{11} > \alpha_{12}$ and $\alpha_{22} > \alpha_{21}$. Taking the product of these two inequalities yields $\alpha_{22}\alpha_{11} > \alpha_{12}\alpha_{21}$ (see SI2.2), which is the condition for stabilisation. Hence, these comparisons in combination are a sufficient (though not necessary) condition to demonstrate stabilisation. However, the comparisons $\alpha_{11} > \alpha_{12}$ and $\alpha_{22} > \alpha_{21}$ differ crucially from the conditions for stable coexistence (eqn 3) because the wrong competition coefficients are being compared. A finding that per capita effects *of* conspecifics are more negative than per capita effects *of* heterospecifics for both species is consistent with both competitive exclusion and stable coexistence (compare Figs 2b and 3b). Further, a finding that the condition is not met for one of the two species does not preclude stable coexistence or stabilisation, because these are not *necessary* conditions for stabilisation (e.g. Fig. 4b, compare with Fig. S1b). However, failure to meet both conditions is sufficient to demonstrate lack of stabilisation (e.g. Fig. S2b). (See Appendix S2, section 2.1.2, for mathematical details.)

Because the theoretical conditions for stable coexistence involve comparisons of effects *on* conspecifics with effects *on* heterospecifics, we might expect that comparing the per capita effects *on* conspecifics vs. *on* heterospecifics would be more informative ($1 \rightarrow 1$ vs. $1 \rightarrow 2$ and $2 \rightarrow 2$ vs. $2 \rightarrow 1$), Table 1, Type 1C). Such a comparison is performed by Ramage & Mangana (2017). They measure the effect of mature American beech abundance on the establishment of both conspecific seedlings as well as heterospecific seedlings. Again, assuming this is a proxy for per capita population growth rates, the corresponding tested conditions for the two-species Lotka–Volterra competition model are $r_1\alpha_{11} > r_2\alpha_{21}$ and $r_2\alpha_{22} > r_1\alpha_{12}$. Taking the product of these inequalities and simplifying again yields the condition for stabilisation. However, satisfying these inequalities does not satisfy the conditions for stable coexistence, because the intrinsic rates of increase (r_1 and r_2) cannot be cancelled from these inequalities individually. This confounding with r prevents conclusions regarding stable coexistence from comparisons of slopes alone, as classically recognised by Bender *et al.* (1984). When Chesson (2018) refers to the need to appropriately “scale” the response of per capita population growth rates, he is referring to the need to factor out these r 's. A finding that per capita effects *on* conspecifics are more negative than per capita effects *on* heterospecifics is thus consistent with both competitive exclusion and stable coexistence (compare Figs. 2c and 3c). Further, a finding that these conditions are not met for one of the two species does not preclude stable coexistence or stabilisation,

because they are not *necessary* conditions given the confounding with r 's (e.g. Fig. 4c, compare with Fig. S1c). However, failure to meet both conditions is sufficient to demonstrate lack of stabilisation (e.g. Fig. S2c). (See appendix S2, section 2.1.3, for mathematical details.)

Thus, standard analyses comparing the strength of conspecific and heterospecific negative density-dependence for a two-species system enable qualitatively the same conclusions regardless of whether they compare effects *on* or effects *of* conspecifics vs. heterospecifics (Table 1, compare Type 1B and 1C). Regardless of the comparisons being performed, finding stronger negative effects for conspecifics than heterospecifics in both species is a sufficient but not necessary condition for stabilisation, and does not provide further information on stable coexistence. However, the same types of data commonly used for such analyses have the potential to be used instead for analyses in which the r 's and α 's are estimated separately, enabling direct tests of stable coexistence, as discussed in the section *Ways forward*.

Frequency-dependence studies

Studies of frequency dependence quantify performance of a focal species as a function of its frequency (focal species density divided by total density of all species), instead of as a function of its density (Table 1; study type 2). The frequency of a focal species changes when its own density and/or that of competing species (in aggregate) changes.

Most commonly, frequency-dependence is evaluated in the context of an experimentally imposed fixed total density of the interacting species (study type 2A in Table 1). For example, Harpole & Suding (2007) sowed seeds of pairs of species at varying frequencies in multiple plots, constrained by a fixed total seed mass per plot, and investigated how the estimated per capita population growth rate of each species (scaled by the total seed production) varied with its initial frequency. If we assume this resulted in a fixed total density, N_{tot} , then testing for negative frequency-dependence from the slopes they evaluated corresponds to testing $r_1(\alpha_{11} - \alpha_{12})N_{tot} > 0$ and $r_2(\alpha_{22} - \alpha_{21})N_{tot} > 0$ in the Lotka–Volterra competition model. Negative frequency-dependence for both species under a fixed total density thus demonstrates $\alpha_{11} > \alpha_{12}$ and $\alpha_{22} > \alpha_{21}$. Together these constitute a sufficient, though not necessary, condition for stabilisation, but they do not constitute a necessary or sufficient condition for stable coexistence, as they involve the wrong comparisons of competition coefficients (And in this case, the individual competition coefficients cannot be estimated from the measured quantities and rearranged into the correct comparisons, unlike in studies of density-dependence). Even when such studies find positive population growth rates for both focal species at low conspecific frequency, this does not generally indicate a positive invasion growth rate unless the total density used is equal to the carrying capacity of the competing species. A finding of negative frequency-dependence for both species given constant total density is consistent with both stable coexistence and competitive exclusion (e.g. Figs. 2d and 3d both show negative frequency-dependence, though the first involves stable coexistence and the second competitive exclusion). Further, a

finding of positive frequency-dependence for one species and negative frequency-dependence for the other is consistent with stable coexistence (e.g. Fig. 4d), competitive exclusion despite stabilisation, and competitive exclusion without stabilisation (e.g. Fig. S1d). Finding positive frequency-dependence for both species is sufficient to demonstrate a lack of stabilisation (e.g. Fig. S2) (See Appendix S2, section 2.2.1, for mathematical details).

Adler *et al.* (2007) introduced a very specific case of frequency-dependence analyses, in which the density of the competing species is always at its equilibrium abundance given the varying densities of the focal species (Table 1; study type 2B). That is, density combinations are chosen by varying the density of the focal species and simultaneously setting the density of the competing species to the value at which it has a zero population growth rate given the density of the focal species. In this analysis of frequency-dependence, the total density is thus not necessarily constant (Figs. S5–S7). For this special set of density combinations, finding negative frequency dependence indicates $\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21} > 0$, which is the condition for stabilisation in the Lotka–Volterra model. Thus such a finding is a necessary and sufficient condition for stabilisation (compare Figs. S5 and S6 with S7). If in addition the per capita population growth rate crosses zero at a frequency between 0 and 1, then this also constitutes a necessary and sufficient condition for stable coexistence (compare Figs. S5 and S6). (See Appendix S2, section 2.2.2, for mathematical details.) In practice, evaluating this particular type of frequency-dependence is extremely challenging as it is difficult to achieve all the required combinations of densities, as some are highly unstable (e.g. some involve densities that are larger than the carrying capacities). We are not aware of any empirical study applying this approach.

Plant–soil feedback studies

Studies of plant–soil feedback quantify the performance of one or more plant species in soils cultured by monocultures of conspecifics or heterospecifics, or directly in monocultures of conspecifics and heterospecifics. Our analysis of how these studies relate to conditions for stabilisation and stable coexistence assumes that competitive effects of one plant species on another operate primarily through soil micro-organisms, such that differences in performance between soils cultured by monocultures of different species are equivalent to differences in performance in monocultures themselves.

These studies do not measure the response of species to a density- or frequency-gradient and thus do not allow estimation of per capita effects. These studies instead effectively estimate total effects of conspecifics ($1 \rightarrow 1$ and $2 \rightarrow 2$) and heterospecifics ($1 \rightarrow 2$ and $2 \rightarrow 1$) at whatever densities are used for the monocultures. In terms of analyses, we can divide these studies into two classes: those comparing the total effects *of* conspecifics and heterospecifics (e.g. Connell 1984; Klironomos 2002; Petermann *et al.* 2008; Yamazaki *et al.* 2009) and those comparing the total effects *on* conspecifics and heterospecifics (e.g. Alvarez-Loayza & Terborgh 2011).

Petermann *et al.* (2008) provides an example of a study comparing total effects *of* conspecifics and heterospecifics

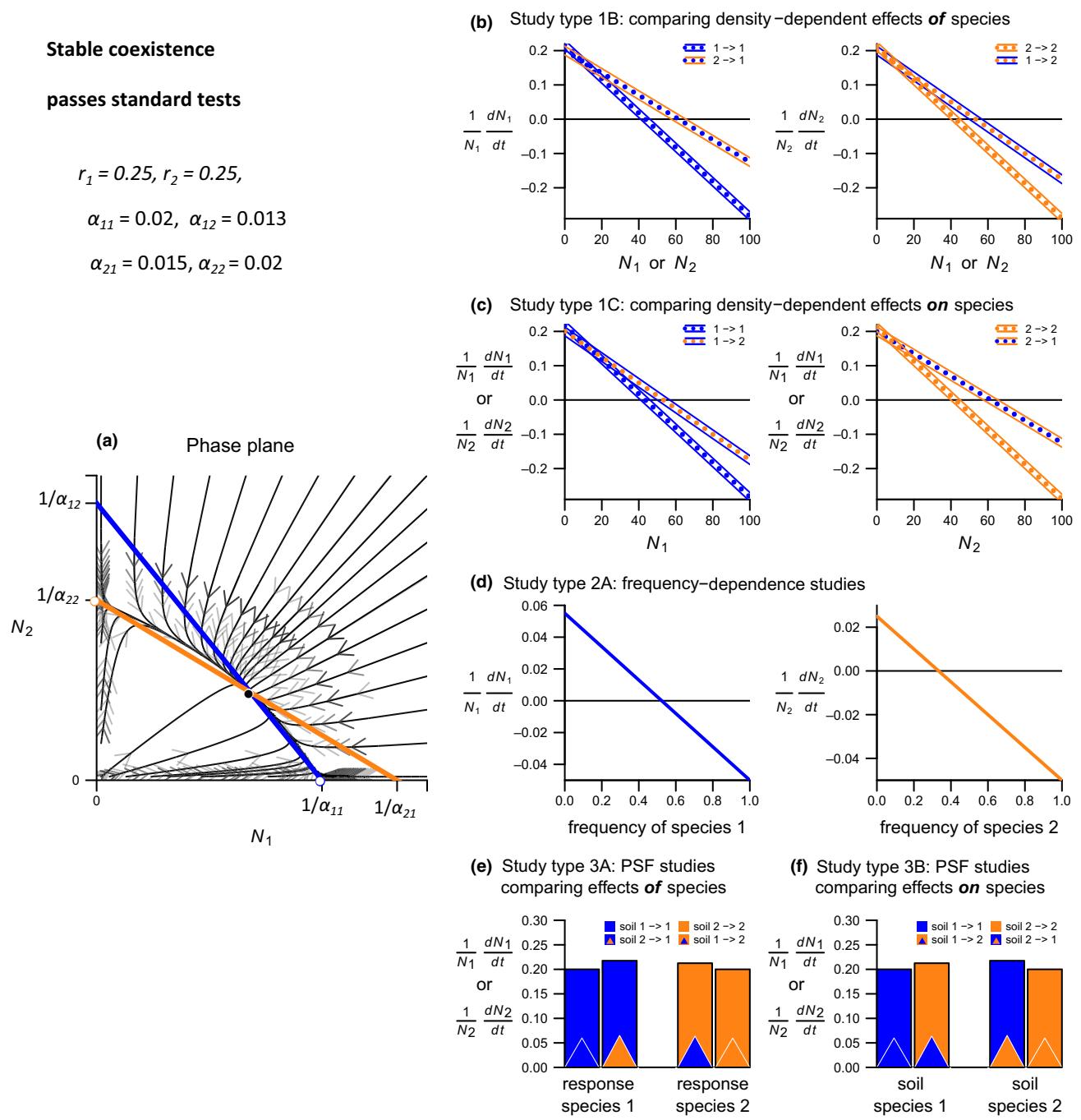


Figure 2 Phase plane (a) for a scenario of stable coexistence of two competing species (as in Figure 1a), together with empirical results (b–f) that would be obtained for this scenario under several types of studies. For this particular set of parameters, common empirical analyses would find patterns considered signatures of stabilisation: stronger negative density-dependent effects *of* conspecific species than *of* heterospecific species for both species (b), stronger negative density-dependent effects *on* conspecific species than *on* heterospecific species for both species (c, note the difference in axis titles compared to b), negative frequency dependence when the total density is constant for both species (d), stronger total negative effects *of* conspecifics than *of* heterospecifics in plant–soil feedback studies for both species (e) and stronger total negative effects *on* conspecific species than *on* heterospecific species in plant–soil feedback studies for both species (f). Note that qualitatively similar empirical results would not necessarily be found for other parameter combinations yielding stable coexistence, as none of these patterns are necessarily present given stable coexistence (Table 1, compare Fig. 4).

(Table 1, Type 3A). They grew 24 European grassland species in soils conditioned by monocultures of conspecifics or monocultures of one heterospecific species, and found that species on average had 30% lower biomass when grown on soil conditioned by conspecifics. In the two-species Lotka–Volterra

competition model, this translates to a finding that $r_1(1 - \alpha_{11}N_1) < r_1(1 - \alpha_{12}N_2)$ and $r_2(1 - \alpha_{22}N_2) < r_2(1 - \alpha_{21}N_1)$. Taking the product of these two inequalities and cancelling yields the condition for stabilisation. However, such results do not test the conditions for stable coexistence

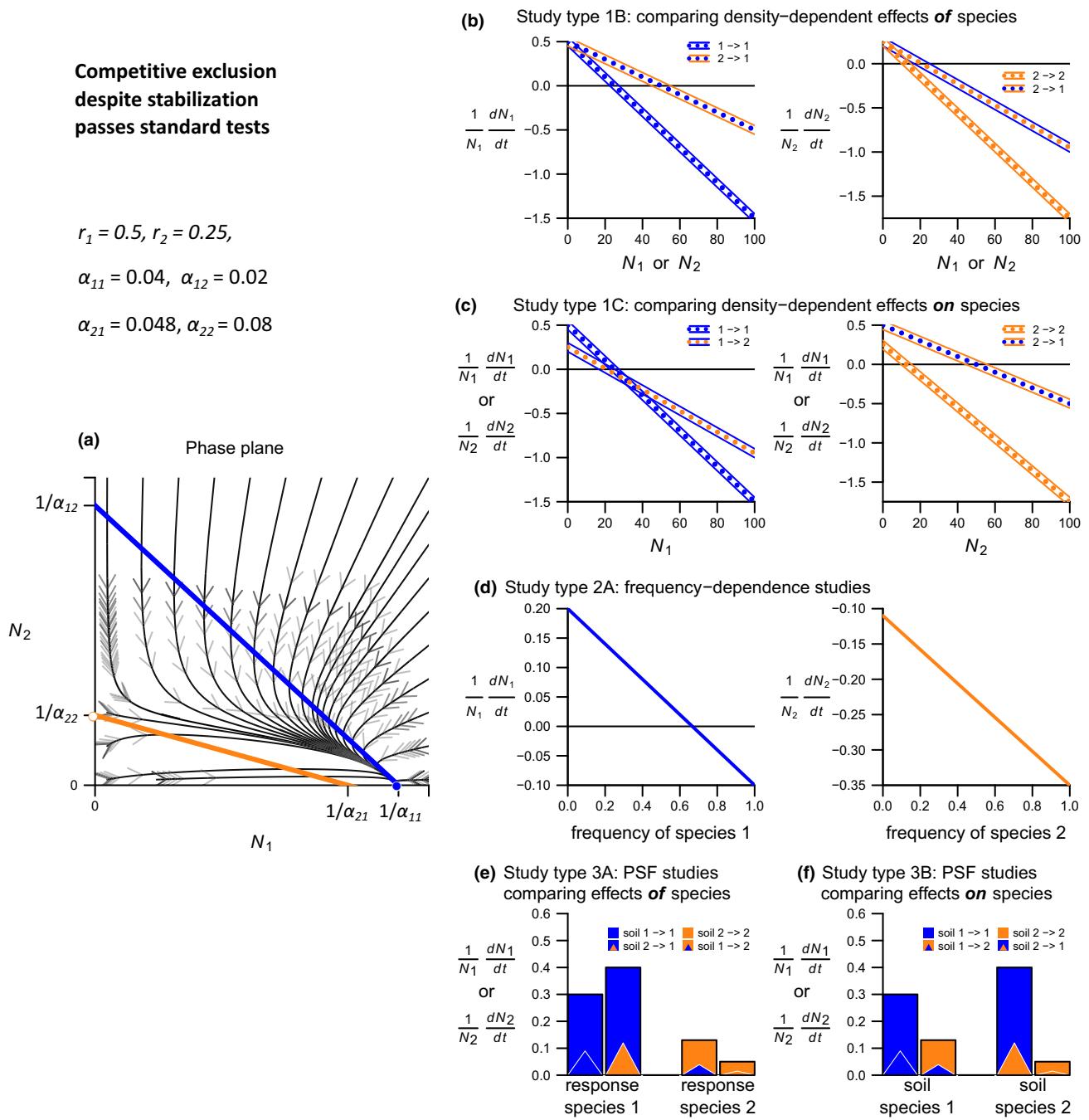


Figure 3 Phase plane (a) for a scenario of competitive exclusion of species 2 by species 1 despite stabilisation (as in Figure 1b), together with empirical results (b–f) that would be obtained for this scenario under several types of studies. For this particular set of parameters, common empirical analyses would find patterns considered signatures of stabilisation: stronger negative density-dependent effects *of* conspecific species than *of* heterospecific species for both species (b), stronger negative density-dependent effects *on* conspecific species than *on* heterospecific species for both species (c), negative frequency dependence when the total density is constant for both species (d), stronger total negative effects *of* conspecifics than *of* heterospecifics in plant–soil feedback studies for both species (e) and stronger total negative effects *on* conspecific species than *on* heterospecific species in plant–soil feedback studies for species 2, but not for species 1 (f). Note that qualitatively similar empirical results would not necessarily be found for other scenarios of competitive exclusion despite stabilisation, as none of these patterns are necessarily present given stabilisation or even stable coexistence (Table 1, compare Fig. 4).

($\alpha_{22} > \alpha_{12}$ and $\alpha_{11} > \alpha_{21}$) because the population densities cannot be cancelled out of the inequalities, and because the wrong competition coefficients are compared. A finding that total effects *of* conspecifics are more negative than total effects *of* heterospecifics in both species is consistent with competitive exclusion despite stabilisation as well as with stable

coexistence (compare Figs. 2E and 3e). Further, a failure to find such negative feedback in one of two species is also consistent with both competitive exclusion and coexistence, because of the confounding with r 's and N 's (e.g. Figs. 4e, and more clearly in Fig. S3e, compare with Figs. S1e). Finding positive feedback in both species is sufficient to establish

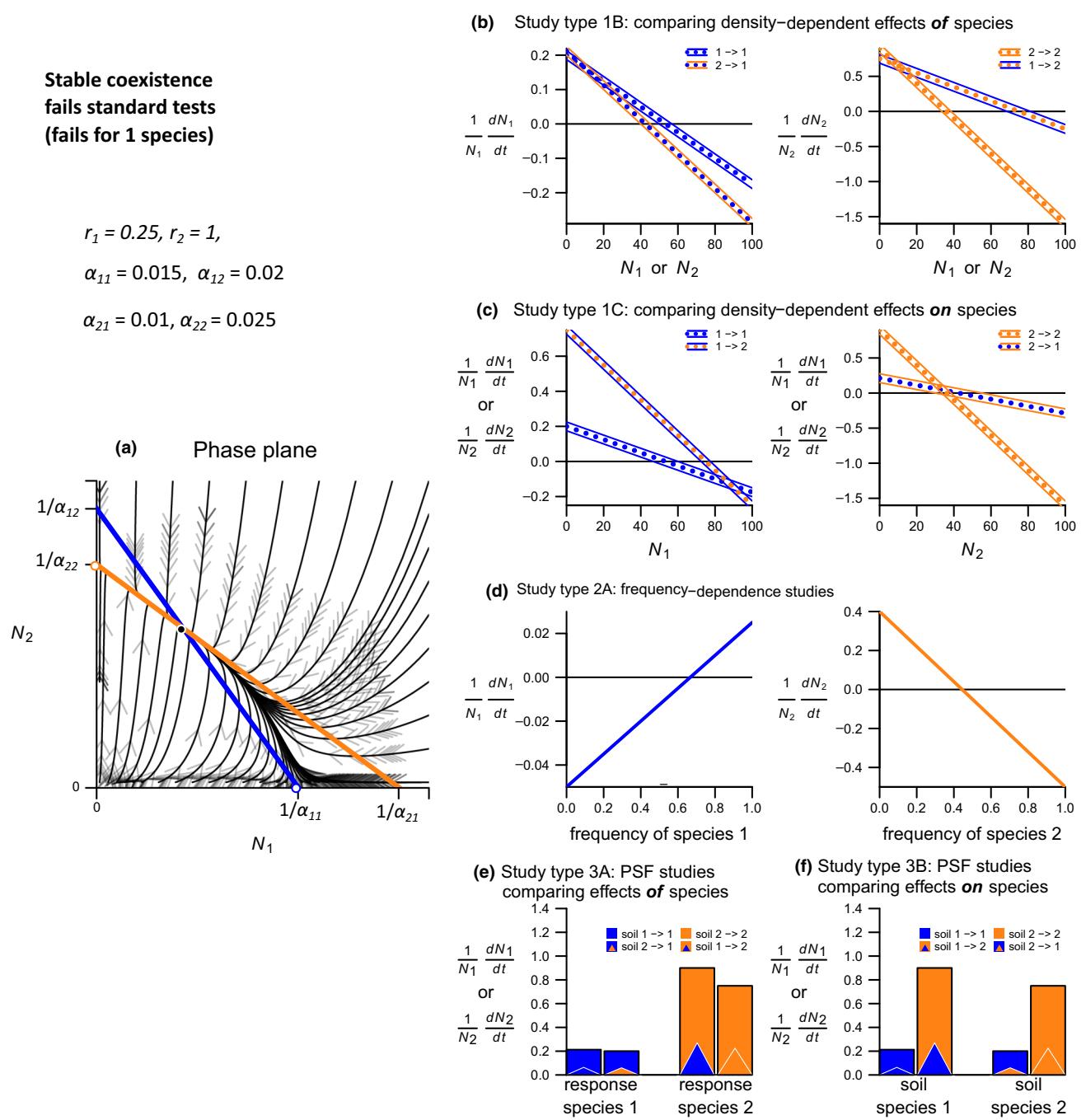


Figure 4 Phase plane (a) for a scenario of stable coexistence of two competing species (as in Figure 1a), together with empirical results (b–f) that would be obtained for this scenario under several types of studies. For this particular set of parameters, common empirical analyses would find patterns considered indicators of a lack of stabilisation: weaker negative density-dependent effects *of* conspecifics than *of* heterospecifics for species 1 (b), weaker negative density-dependent effects *on* conspecifics than *on* heterospecifics in both species (c), positive frequency dependence of species 1 (d), weaker total negative effects *of* conspecifics than *of* heterospecifics in plant–soil feedback studies for species 1 (e), and weaker total negative effects *on* conspecifics than *on* heterospecifics in species 2 (f). This contrasts with the scenario in Figure 2, in which qualitatively the opposite patterns were found for another stable coexistence scenario.

lack of stabilisation (e.g. Fig. S2e). (See Appendix S2, section 2.3.1, for mathematical details.)

Paradoxically, comparing total effects *on* conspecifics and heterospecifics turns out to be even less informative (Table 1, Type 3B). For example, Alvarez-Loayza & Terborgh (2011) evaluated survival of conspecific and heterospecific seedlings

growing under crowns of canopy tree species in a tropical forest, and found that conspecific survival was much lower. Assuming seedling performance is in this case a proxy for per capita population growth rate and treating heterospecifics as though they are a single competing species (see *Critical assumptions and limitations of these linkages*), this translates to

the finding that $r_1(1 - \alpha_{11}N_1) < r_2(1 - \alpha_{21}N_1)$ and $r_2(1 - \alpha_{22}N_2) < r_1(1 - \alpha_{12}N_2)$. This cannot be rearranged into a condition for stabilisation or stable coexistence, due to the confounding influences with r 's and N 's. As a result, the tested inequalities correspond to neither necessary nor sufficient conditions for stabilisation or species coexistence. A finding that total effects *on* conspecifics are more negative than total effects *on* heterospecifics in both species is consistent with both competitive exclusion and stable coexistence, and indeed even with competitive exclusion in a system lacking any stabilisation (e.g. Figs. 2f, S1f and S4f). Failure to meet this pair of conditions is also consistent with both stable coexistence and competitive exclusion (Figs. 3f, 4f and S2f) (See Appendix S2, section SI2.7, for mathematical details).

Critical assumptions and limitations of these linkages

In the preceding section, we linked commonly performed empirical tests with the basic conditions for stabilisation and stable coexistence in the two-species Lotka–Volterra competition model. In doing so, we glossed over a number of implicit assumptions that limit the conclusions that can be drawn from many such analyses in practice. Here we detail these critical assumptions and associated limitations. In particular, we address the use of individual vital rates as proxies for per capita population growth, the connection between coexistence conditions for pairs of species and coexistence conditions for multi-species communities, and the central assumption that the model adequately describes real-world dynamics. The limitations detailed here apply to what can be learned from these studies regarding stabilisation or stable coexistence in the pairwise framework. These considerations do not generally limit conclusions regarding different objectives that may have motivated the original studies, such as the quantification of negative density-dependence in and of itself.

First, all model criteria for stabilisation or stable coexistence concern per-capita population growth rates (eqn 1). However, the vast majority of empirical studies measure only a single vital rate at a single life stage, and hardly any address all vital rates at all life stages. Effects on individual vital rates at a single life stage are not equivalent to effects on per capita population growth rates. Vital rates and life stages make unequal contributions to per capita population growth (de Kroon *et al.* 2000) and effects at one life stage can be offset at another (Moll & Brown 2008; Gonzalez *et al.* 2013; Visser *et al.* 2016). Because stable coexistence depends on niche differences exceeding fitness differences, and because total niche differences and fitness differences will almost invariably depend on multiple life stages and vital rates, there is little point in attempting to test conditions for stable coexistence based on analyses for a single life stage and vital rate. Studies on only a subset of life stages and vital rates cannot establish if there is stable coexistence over the life cycle as a whole, or quantify overall stabilisation. However, studies on a single vital rate and life stage can quantify stabilisation at the focal life stage and vital rate (i.e. the presence of niche differences). If there is no positive density-dependence at other life stages and vital rates, then stabilisation at any life stage or vital rate necessarily implies stabilisation of the per capita population

growth rates (provided the focal vital rate and life stage has non-zero elasticity, that is, it makes a non-zero contribution to per capita population growth rates).

Second, the theoretical conditions we reference apply only to two-species systems, and do not enable firm conclusions for more diverse communities. Some studies of multi-species communities have pooled all heterospecifics as a single unit, effectively treating them as a second species (e.g. Comita *et al.* 2010; Johnson *et al.* 2012). The resulting estimated interspecific terms are averages of many competing species, and do not allow definitive conclusions for the community as a whole or any two-species subset (see Appendix S3). Other studies have evaluated every pair of species (e.g. McCarthy-Neumann 2010a, 2010b). Unfortunately, theory demonstrates that three species may coexist even if none of the pairwise combinations stably coexist (e.g. intransitive competition, Levine *et al.* 2017) and three species may fail to coexist even if all pairwise combinations stably coexist (e.g. Barabas *et al.* 2016). This phenomenon is not merely theoretical: Kraft *et al.* (2015) evaluated conditions for stable coexistence in 102 pairs of 18 different species that coexist at the landscape scale, and found that conditions for stable coexistence were met for only 12 species pairs. Nonetheless, stable coexistence of pairs of species within a community makes coexistence of larger species assemblages more likely, whereas competitive exclusion for pairs of species makes multispecies coexistence less likely in a variety of models (e.g. Barabas *et al.* 2016; Adler *et al.* 2018; Chesson 2018), as well as in real microbial communities (Friedman *et al.* 2017).

Finally, the implicit assumption from meeting conditions for stabilisation or stable coexistence that correspond with the Lotka–Volterra model (Table 1) is that the model provides a sufficiently good representation of the real-world dynamics. Similarly, conclusions based on conditions under another model depends on that model being a sufficiently good fit. Needless to say, there are many ways in which real-world communities can deviate from the Lotka–Volterra model, or any other simple competition model. Standard models are time-invariant and spatially uniform, yet temporal and/or spatial environmental variation can stabilise or destabilise communities (e.g. Chesson 1994; Angert *et al.* 2009). Standard models are written in terms of equations for average densities, yet limited dispersal may structure the spatial arrangements of conspecific and heterospecific individuals and alter the outcome of competition (e.g. Pacala & Levin 1997; Bolker *et al.* 2003). Populations may be size-structured, and the strength of competitive effects and responses may vary not only with species identity, but also with individual size (e.g. Comita *et al.* 2010; Uriarte *et al.* 2010). If a model is fundamentally inadequate to describe a community, then analyses based on that model will not reliably indicate the presence or absence of stabilisation and stable coexistence in the focal community.

WAYS FORWARD

In this section, we discuss two alternative approaches to evaluating coexistence conditions: invasibility experiments and model parameterisation studies.

Invasibility experiments

Invasibility experiments directly evaluate the invasibility criterion, and are often recommended as a straightforward alternative for testing stable coexistence (e.g. Siepelski & McPeek 2010; Germain *et al.* 2018). The invasibility criterion requires that each species have a positive invasion growth rate, that is, that it is able to increase from low abundance when the rest of the community is at its equilibrium in the absence of the focal species. Experimental tests thus require first allowing the resident community in the absence of the focal species to reach its equilibrium abundance, and then introducing the focal species and following it over time to evaluate if it can increase in abundance (Fig. 5). Successful experimental tests of the invasibility criterion have been performed for algae (Narwani *et al.* 2013; Venail *et al.* 2014), bacteria (Tan *et al.* 2017; Li *et al.* 2019), yeast (Grainger *et al.* 2019), cyanobacteria (Gallego *et al.* 2019) and amphipods (Cochran *et al.* 2015), among others. These are all relatively small, short-lived taxa; invasibility experiments become increasingly infeasible for larger and longer-lived organisms (Siepelski & McPeek 2010).

Unfortunately, mutual invasibility is not necessarily a reliable indicator of stable coexistence for communities with complex dynamics and/or more than two species (Law & Morton 1996; Barabas *et al.* 2016; Chesson 2018). In general, invasibility is not a *necessary* condition for species coexistence, because a variety of mechanisms can lead species to fail invasibility tests even though they stably coexist. For example, species with strong Allee effects display negative population growth rates below a critical population size, even though they have positive population growth rates at larger sizes (Courchamp *et al.* 1999). For communities of more than two species, invasibility is not even a sufficient condition for stable coexistence, because successful invasion can lead to extinction of one of the resident species (Law & Morton 1996). Of course, this particular problem could be circumvented by extending invasibility experiments for longer periods of time, and verifying that all species are able to coexist stably after invasion.

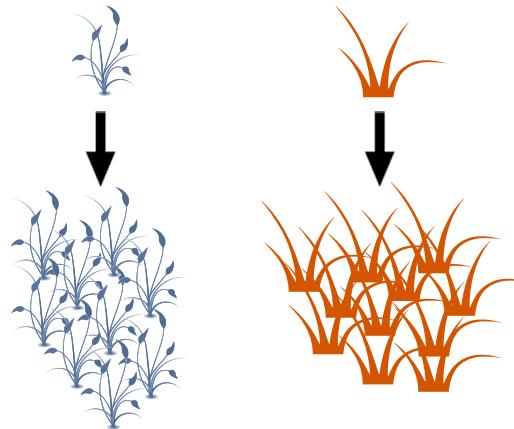
The same taxa that are amenable to invasibility experiments are also amenable to other experimental density manipulations that could directly measure the dynamics of the phase plane (e.g. Fig. 6a and b). Such experiments could evaluate local stability of hypothesised coexistence equilibria or even assess the more complicated “permanence” condition for stable coexistence under complex dynamics (Law & Morton 1996). Such experiments have the advantage that they do not presume any particular model for species coexistence. In practice, evaluating coexistence conditions with experiments alone becomes increasingly impractical for more diverse communities with more complex dynamics, as possible density combinations increase with the power of the number of species. However, such experiments can potentially be incorporated into a model parameterisation approach, which is discussed in the next section.

Model parameterisation studies

Under the model parameterisation approach, empirical data are used to parameterise a model of species interactions,

- (a) Grow communities without the focal species until they reach their equilibrium abundances**

Community 1
(no species 2)
Community 2
(no species 1)



- (b) Introduce the focal species into each community and measure its population growth rate**

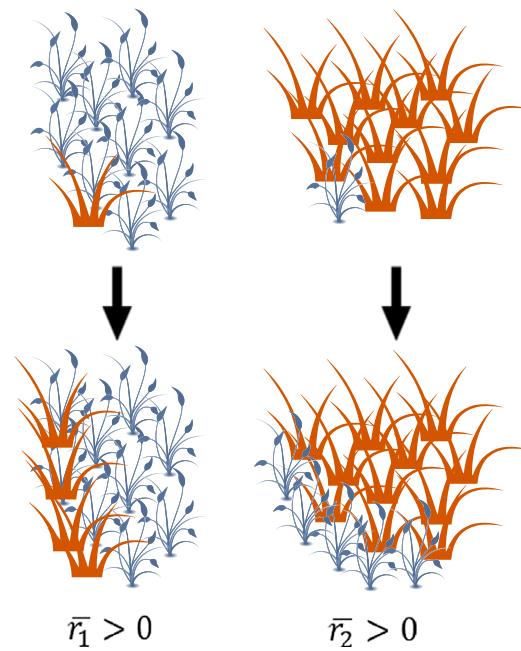


Figure 5 Schematic of experimental tests of the invasibility criterion, a sufficient condition for stable coexistence.

which is then used to test theoretical conditions for stabilisation and/or stable coexistence (Fig. 6). Levine & HilleRisLambers (2009) pioneered this approach, which has since been applied in multiple studies (e.g. Adler *et al.* 2010, Godoy & Levine 2014; Godoy *et al.* 2014; Chu & Adler 2015; Kraft *et al.* 2015; Chung & Rodgers 2016; Germain *et al.* 2016; Cardinaux *et al.* 2018; Petry *et al.* 2018; Hart *et al.* 2019). Beyond testing conditions for coexistence, this approach can also link dynamics with underlying mechanisms (e.g. resource

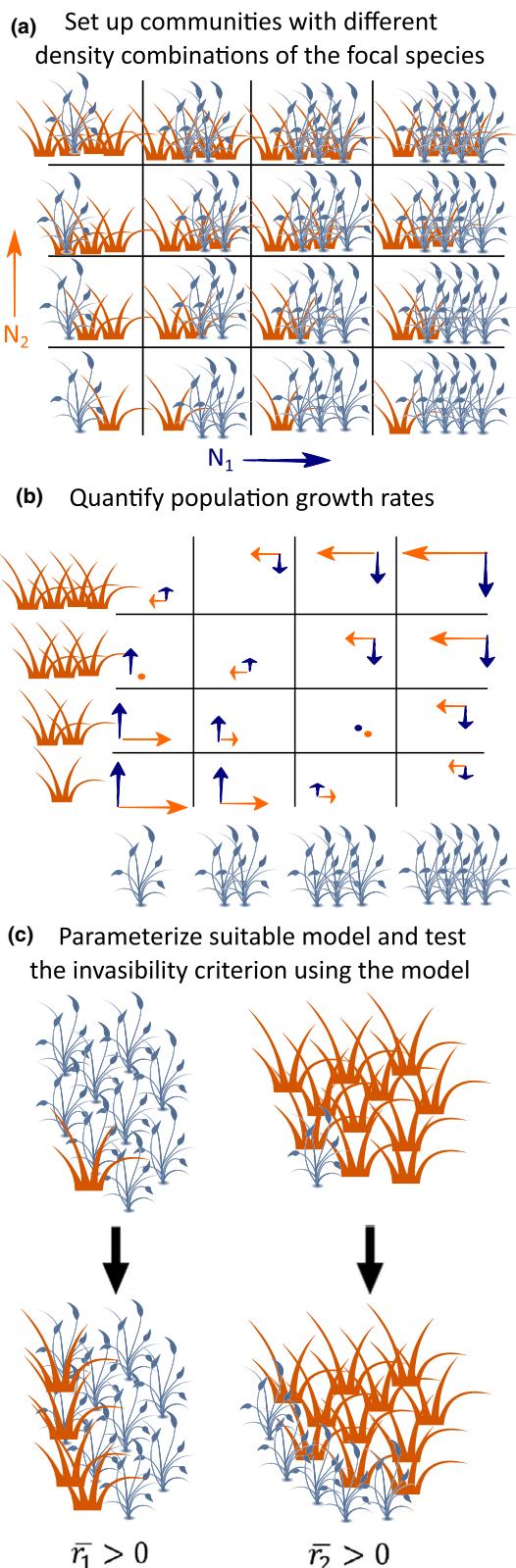


Figure 6 Schematic of one possible type of model parameterisation study involving two species with short generation times. Population growth rates of both species are measured for multiple combinations of densities. These data are used to parameterise a competition model, which enables analytical or numerical results on stable coexistence, for example, by calculating the invasion growth rates as shown here.

competition, natural enemies), evaluate the sensitivity of dynamics to different processes (e.g. those acting on reproduction vs. those acting on growth), and quantify niche differences and fitness differences (Box 2). The model parameterisation approach can accommodate complex dynamics through appropriate choice of models, and it can be applied to long-lived and large-statured organisms.

As an example, Chung & Rudgers (2016) applied this approach to two arid land grass species. They measured the biomass accumulation of each species at 15 different combinations of densities, fit the Beverton–Holt model to the data with maximum likelihood estimation, and then used the estimated parameters (competition coefficients and intrinsic rates of increase) to calculate the invasion growth rates and evaluate evidence for stable coexistence with and without rhizosphere inoculation with soil microbes. They showed that both species can invade a community of the other species and thus stably coexist when associated microbes are present, but one was unable to invade when they were absent. Thus, this study not only demonstrated stable coexistence, but established the importance of a particular underlying mechanism.

In some cases, models can be parameterised with very much the same kinds of data typically collected in studies of density-dependence, frequency-dependence, or plant–soil feedback, enabling greater insights to be gleaned from these data sets. For example, suppose we have data for per capita population growth rates of two species growing at many density combinations, in a two-species system that conforms to the Lotka–Volterra competition equations. If we analyse these data as in traditional tests of negative density-dependence, then we will estimate the slopes of each species's response to conspecifics and heterospecifics, compare the slopes, and at best find sufficient evidence for stabilisation of the two-species interactions. In a model parameterisation framework, we would estimate the intercepts as well, recognising that these intercepts represent the intrinsic rates of increase (r_1, r_2). We would also recognise that the slopes are the products of the intrinsic rates of increase and the competition coefficients (α_{ij}), and thereby use the combination of the intercepts and slopes to estimate all four competition coefficients. In this case, the competition coefficients can be obtained simply by dividing the slopes by the intercepts (this amounts to “rescaling” the per capita population growth rates to obtain what Chesson (2018) refers to as the “natural-scale growth rates”). We can then directly test the condition for stable coexistence (eqn 3) as well as the condition for stabilisation (eqn 4).

The model parameterisation perspective also helps us to interpret variation in fitted parameters of negative density-dependence and similar analyses. For example, a number of studies compare regression coefficients for conspecific and heterospecific effects – essentially the estimated slopes of the relationships of per capita performance to density – across species (e.g. Comita *et al.* 2010, Zhu *et al.* 2018). For the Lotka–Volterra model, these slopes are the products of r_i (here the “potential” performance at low density of competitors) and the associated competition coefficients (α_{ij}), as noted above. These r_i vary systematically with life history – for example, light-demanding tree species typically have faster

individual growth rates, lower survival rates, and higher intrinsic rates of population growth in the absence of competition. Thus, differences in r_i will affect differences in “strength of conspecific negative density-dependence” measured as such regression coefficients, even though differences in r_i are not relevant for stabilisation and coexistence in the Lotka–Volterra model. Appropriately fitting a suitable (for the data) model would clarify these distinctions, and provide a better basis for evaluating links with species characteristics, among other things.

Challenges of long-lived organisms and high-diversity systems

The model parameterisation approach can be applied to complex models such as those incorporating multiple life stages, size structure, spatial interactions and/or temporally varying environments. Annual plant models may include separate terms for seed production, seed survival, and seed germination rate (e.g. Angert *et al.* 2009; Levine & HilleRisLambers 2009; Godoy & Levine 2014; Godoy *et al.* 2014; Kraft *et al.* 2015; Petry *et al.* 2018). Species with size-structured competition and substantial variation in size may benefit from size-structured models, such as integral projection models (Merow *et al.* 2014). Localised competitive interactions may be captured in spatially explicit, individual-based models. For example, Adler *et al.* (2010) and Chu & Adler (2015) performed regression analyses to estimate conspecific and heterospecific density effects on the survival, growth and recruitment rates of four plant species. They used these estimated parameters to build population models for each species, and then ran simulations to quantify invasion growth rates – which were all positive – and thereby establish stable coexistence. Of course, a critical challenge with making models more complex is that more data are needed to obtain good parameter estimates (Carrrara *et al.* 2015).

In high diversity systems, fitting competition models in which there is one parameter for every pair of species rapidly becomes infeasible as diversity increases, because the number of parameters increases with the square of species richness. An alternative is to fit more mechanistic models in which parameters represent species-specific interactions with resources, responses to conditions, competitive effects (e.g. shading), and/or competitive responses (e.g. shade-tolerance). This category includes a wide variety of models (e.g. MacArthur 1970; Pacala *et al.* 1996; Chase & Leibold 2003; Farrior *et al.* 2013; Letten *et al.* 2017; Ellner *et al.* 2019). In such models, parameter number increases in proportion to species richness, rather than with the square of richness, limiting parameter numbers as diversity increases. However, even with these models, a single bad parameter estimate can create a “superspecies” that competitively excludes all others (Pacala *et al.* 1996). Approaches that relate species parameters to functional traits (McGill *et al.* 2006; Kunstler *et al.* 2016) or constrain them based on known tradeoffs (Clark *et al.* 2018) can reduce the scope for such errors. The contributions of different mechanisms to coexistence can then be quantified numerically from the model using the methods of Ellner *et al.* (2019).

CONCLUSIONS AND FUTURE DIRECTIONS

Ecologists have published many studies of density-dependence, frequency-dependence, and plant soil-feedback. These studies have provided many important insights, for example, in showing how particular niche axis and/or groups of natural enemies contribute to the strengths of intra- vs interspecific competition (e.g. Packer & Clay 2000; Petermann *et al.* 2008; Bagchi *et al.* 2010). In this review, we evaluated the evidence for stabilisation and stable coexistence provided by the analyses typically performed in such studies, and considered how we can glean more knowledge of these subjects from these types of studies. For each of the standard types of analyses of density-dependence, frequency-dependence and plant-soil feedback, we precisely specified the equivalent tested condition under the two-species Lotka–Volterra and Beverton–Holt competition models, and established how these tests relate to conditions for stabilisation and stable coexistence of pairs of species in these models.

Our analyses show that the tested conditions of most analyses of negative density-dependence, negative frequency-dependence, and negative plant-soil feedback constitute sufficient conditions for stabilisation under the Lotka–Volterra two-species competition model. Thus, if the data concern per capita population growth rates of two species, such tests can demonstrate stabilisation of the focal species pair. If the data concern performance at a particular life stage or vital rate, then findings of stabilisation increase the likelihood that per capita population growth rates as a whole are stabilised, especially if pre-existing knowledge indicates that it is unlikely that there is positive density-dependence at any other life stage or vital rate. Such findings indicative of stabilisation make stable coexistence more likely, by expanding the parameter space consistent with stable coexistence (even for multi-species systems). However, even where the tested conditions are sufficient conditions for stabilisation, they are not necessary conditions in addition, meaning that failure to meet the conditions does not constitute evidence against stabilisation. Further, the tested conditions are for the most part neither sufficient nor necessary conditions for stable coexistence. And importantly, findings of stabilisation for pairs of species do not translate to any definitive conclusions for communities of more than two species.

In recent years, many studies have moved from simply testing for negative density-dependence and similar conditions to a model parameterisation framework in which such data are applied to estimating parameters of a specified model for species interactions. Provided the model is an appropriate description of the system, this approach enables direct tests of conditions for stabilisation and stable coexistence, either analytically or numerically (i.e. with simulations). For many communities of long-lived organisms and/or high species richness, design and parameterisation of a model that appropriately captures interactions throughout the life cycle to fully capture mechanisms of coexistence remains a distant dream. Yet even for these communities, a model-parameterisation perspective can help us to better link processes to mechanisms, evaluate their relative importance, and advance our understanding of coexistence. Our analysis makes such links clear, and will we

hope help inform future studies in ways that increase the insights they provide.

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The original idea was conceived by HdK, HM-L, MDV, SJW and EJ. The analyses were done by MJEB, MDV, HdK and HM-L, the mathematical derivations by MJEB, and the figures were made by MJEB, MDV and HM-L. MJEB, HM-L and HdK wrote the paper, with substantial input from all authors.

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No data were used.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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