**Indirect effects of environmental change in resource competition models**

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**Abstract:**

Anthropogenic environmental change can affect species directly by altering physiological rates or indirectly by changing competitive outcomes. The unknown strength of competition-mediated indirect effects makes it difficult to predict species abundances in the face of ongoing environmental change. Theory developed with phenomenological competition models shows that indirect effects are weak when coexistence is strongly stabilized, but these models lack a mechanistic link between environmental change and species performance. To extend existing theory, we examined the relationship between coexistence and indirect effects in mechanistic resource competition models. We defined environmental change as a change in resource supply points and quantified the resulting competition-mediated indirect effects on species abundances. We found that the magnitude of indirect effects increases in proportion to niche overlap. However, indirect effects also depend on differences in how competitors respond to the change in resource supply, an insight hidden in non-mechanistic models. Our analysis demonstrates the value of using niche overlap to predict the strength of indirect effects and clarifies the types of indirect effects that global change can have on competing species.

**Introduction**

Anthropogenic environmental change affects species directly but also indirectly by altering interactions with predators, pathogens and competitors (Tylianakis et al. 2008). As a result, competition-mediated indirect effects may alter plant and animal community responses to environmental change (Stacey and Fellowes 2002; Jiang and Morin 2004; Brooker 2006; Tylianakis et al. 2008; Adler et al. 2009; Sletvold et al. 2013). In this paper, we define the effects of environmental change at the level of local population density: the direct effect is the sensitivity of a focal species population to some environmental change while holding other species abundances and interaction effects constant; the net effect is the sensitivity of the focal population to environmental change allowing for other species abundances and interactions to change; and the indirect effect is the difference between the net and direct effects (Adler et al. 2012). More specifically, we can define a competition-mediated indirect effect as the difference between the sensitivity of a focal species to environmental change when the influence of competitors is held constant and the sensitivity of a focal species when the influence of competitors is allowed to change along with the changing environment (Fig. 1).

Despite the widespread interest in how global change will affect natural communities, only a handful of studies have controlled for both the mechanism of environmental change and the effects of interspecific competition. Experiments in which both the density of competitors and the global change driver are manipulated are ideal for measuring this kind of indirect effect (Jiang and Morin 2004; Adler et al. 2009; Levine et al. 2010; Eskelinen and Harrison 2013), but the effects of competitors and global change can also be investigated with observational data and statistical and mathematical models (Lemoine and Böhning-Gaese 2003; Poloczanska et al. 2008; Adler et al. 2012). Competition mediated-indirect effects range from strong (Eskelinen and Harrison 2013), to relatively weak (Klanderud 2005; Levine et al. 2010) and can vary depending on the underlying driver of change (Liancourt et al. 2012). The observed variation in the strength of competition-mediated indirect effects suggests that improved theory could help us predict when and where competition is likely to change the net effect of global change on focal populations.

Adler et al. (2012) linked environmental change and competition-mediated indirect effects with coexistence theory. The intuition is straightforward: small niche overlap between competing species implies weak competitive interactions and small indirect effects of environmental change, while large niche overlap implies strong competition and large indirect effects. Adler et al. (2012) supported this argument by analyzing phenomenological competition modelsin which population growth is limited by per capita interspecific (**CF*, *FC) and intraspecific (**FF*, *CC) competition, where the subscript ‘F’ refers to a focal species, and ‘C’ refers to its competitor. Stable coexistence between competitors requires some form of negative frequency dependence, which causes a species’ growth rate to increase when it is rare, and to decrease when it is common (Chesson 2000). Adler et al. (2012) used the strength of negative frequency dependence as a proxy measure for niche overlap: strong negative frequency dependence should indicate low niche overlap between competitors. In both the theoretical models and empirical models parameterized with long-term data from a perennial plant community, they found that the magnitude of indirect effects of climate variation decreased with increasing negative frequency dependence in a perennial plant community.

Although Adler et al. (2012) links coexistence theory with indirect effects of environmental change, their phenomenological competition framework lacks an explicit connection between species performance and environmental conditions. For example, in the theoretical models Adler et al. (2012) used, it seems unrealistic and arbitrary that hypothetical environmental change affects a species’ fecundity but has no effects on other model parameters such as competition coefficients. Models that include the mechanism of competition would provide a more rigorous framework for developing theory about indirect effects and environmental change. In a mechanistic model, a simulated environmental change, such as an increase in resource supply, would simultaneously influence many aspects of performance of both the focal species and its competitor. A second weakness of Adler et al. (2012) is the use of negative frequency dependence as a proxy measure of niche overlap. A more precise measure of niche overlap in terms of phenomenological competition coefficients is given in Chesson (2013 p. 233):

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| --- | --- | --- |
|  |  | (1) |

In this definition niche overlap, , is the geometric mean of interspecific interactions divided by the geometric mean of intraspecific interactions. Stable coexistence is possible only if intraspecific competition is greater than interspecific competition, leading to .

Our goal is to provide a framework for understanding competition-mediated indirect effects that will be useful to ecologists working on empirical studies of global change. Our specific objectives are to link phenomenological definitions of niche overlap to parameters in mechanistic resource competition models and to test the prediction that indirect effects between competitors should be greater when niche overlap is large.

**General Definition of Competition-Mediated Indirect Effects**

As a general example, we start with two functions that give the equilibrium abundances of a focal species and its competitor ,

|  |  |  |
| --- | --- | --- |
|  |  | (2) |

We assume that these equilibrium abundances are in some way determined by the shared resources available in the environment, given by *S*. We are interested in the derivative as a measure of how sensitive the focal species is to a change in the environment. If we assume that both *f* and *g* are continuously differentiable functions we can express their derivatives as a total derivative (Chiang 1984),

|  |  |  |
| --- | --- | --- |
|  |  | (3) |

These equations are immediately useful because they give us the net effects of a change in *S* as the sum of direct effects and indirect effects. The direct effect is the sensitivity of the focal species to a change in *S* while holding the competitor’s abundance constant at the equilibrium and is given by the partial derivative above. We can solve for the derivative of the focal species from the equations in (3),

|  |  |
| --- | --- |
|  | (4) |

This equation gives us the net sensitivity of the focal species to a change in the resource availability, allowing both the competitor and focal species to respond. We define indirect effects as the net effects minus the direct effects, thus we can solve for indirect effects by subtracting the partial derivative from the equation above,

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| --- | --- | --- |
|  |  | (5) |
|  | |  |  |  | | --- | --- | --- | |  |  | (4) | |  |

We now turn to using more explicit functions to model resource uptake and population growth and also consider the relationship with niche overlap.

**Essential Resource Model**

For competing plants, accounting for shared abiotic resources—soil nutrients, water and sunlight—is perhaps the most straightforward way to model competition. These resources are often essential: some amount of the resource must be present for the plant to grow and cannot be substituted by another (Tilman 1982). For instance, a non-parasitic plant requires some amount of light in order to photosynthesize; substituting light with other resources—water, CO2, P—will not mitigate the need for light.

Our two species essential resource competition model follows Tilman (1977; 1982 p. 38). In this model, per-capita growth of the focal species and competitor are determined by the availability of two resources, *R*1 and *R*2, following a saturating Monod function:

|  |  |  |
| --- | --- | --- |
|  |  | (6) |
|  |  |  |

where *r* is the maximum growth rate for each species, *R* is the concentration of each resource, and *m* is a resource loss or mortality rate for each species. The *k* terms determine the concentration of resource one or two for which growth of each species equals half the maximum rate. The larger *k* is the more resource is required for a species to achieve a positive growth rate. Resources are supplied in proportion to the difference between an environmental supply point, *S,* and the current resource concentration, *R*. Resources are taken up by each species in proportion to population growth rate and resource loss/mortality rate (Tilman 1982 p. 46):

|  |  |  |
| --- | --- | --- |
|  |  | (7) |
|  |  |  |

where *a* is a resource turnover rate and the *q*terms (Tilman uses ‘*c*’) give the amount of each resource required for each unit of biomass growth for each species. Each species has a minimum resource requirement for growth and reproduction to balance mortality and loss—this resource requirement defines the zero-net growth isoclines (ZNGI) for the species (Tilman 1982). Coexistence is possible when the ZNGIs cross—meaning that there is a point where each species is limited by a separate resource (Fig. 2). This equilibrium is only stable when each species consumes more of the resource limiting its own growth than it does of the resource limiting its competitor. For example, in Figure 2 the focal species is limited by *R*1 and the competitor is limited by *R*2, and a stable equilibrium requires resource consumption and supply rates described by the inequality (from Tilman 1982, p. 77),

|  |  |  |
| --- | --- | --- |
|  |  | (8) |

In other word, the species can only coexist stably when the resource supply point lies between their resource consumption vectors. Because we are interested in indirect effects produced by competition, we make the assumption that the conditions for coexistence are met.

Equilibrium abundances, and , are reached at resource concentrations and . Assuming the focal species is limited by *R*1 and the competitor by *R*2, we can solve for the equilibrium abundances, and , by setting the differential equations in (7) to zero and setting the resource concentrations to their equilibrium concentrations and .

In Appendix A, we show how Chesson’s measure of niche overlap, , is related to the parameters of Tilman’s essential resource model. Under the assumption that the focal species is limited by resource one and the competitor by resource two,

|  |  |  |
| --- | --- | --- |
|  |  | (9) |

The terms and correspond to each species’ use of the resource it is most limited by, and thus determine intraspecific competition effects. As a result, equation (9) parallels the phenomenological expression for niche overlap in equation (1). If the focal species uses a very different ratio of resources from its competitor, *ρ* will be small, while if it uses a similar ratio of resources, *ρ* will approach one. Graphing resource consumption vectors is an intuitive way to assess niche overlap: generally niche overlap is smaller for a larger angle between species’ resource consumption vectors (Petraitis 1989; Fig. 2) and the greater the area of the parallelogram formed with the resource consumption vectors as sides (Barabás et al. 2014).

*Modeling environmental change*

In a mechanistic resource competition model, we can simulate environmental change as a change in resource supply points, *S*1 or *S*2. This is a reasonable choice in the case of direct addition of essential resources such as phosphorous and nitrogen (Jupp and Spence 1977; Vitousek et al. 1997). It also makes sense when resource supply changes as an indirect consequence of other types of anthropogenic change. For example, global warming can increase availability of soil nitrogen (Nadelhoffer et al. 1991), as can invasion by nitrogen fixing exotic plants (Vitousek and Walker 1989); climate change can alter water availability (Fensham and Fairfax 2007); forest thinning changes light availability to understory species (Thomas et al. 1999); and aquatic invasive species can drive changes in light availability to submerged aquatic plants (Zhu et al. 2006).

For example, if *S*1 represents the supply point for nitrogen in the environment, we can explore the net and indirect effects of anthropogenic nitrogen deposition by calculating the rate of change in focal species abundance, , with respect to *S*1, assuming that other limiting resources such as light are not changing (Dybzinski and Tilman 2007). Once we solve for in the equations above we can then differentiate the full equation to find the net effect of a change in *S*1,

|  |  |  |
| --- | --- | --- |
|  |  | (10) |

Notice that the definition of niche overlap that we derived earlier appears on the right hand side of the equation above, meaning that we can rewrite (10) as,

|  |  |  |
| --- | --- | --- |
|  |  | (11) |

The net sensitivity accounts for the fact that the focal species and competitor can respond to the change in the environment and to each other, achieving new equilibrium abundances. To find the direct effects we hold competitor abundance constant at its previous equilibrium and then find the derivative of the focal species abundance with respect to *S*1 at the resource equilibrium,

|  |  |  |
| --- | --- | --- |
|  |  | (12) |

Note that in this model of resource competition, at equilibrium each species is only sensitive to the direct effects of one resource—Liebig’s law of the minimum (Tilman 1982). In this example, the focal species is sensitive only to *R*1 and the competitor only to *R*2. We can apply the formula for indirect effects by subtracting the direct effects from the net effects,

|  |  |  |
| --- | --- | --- |
|  |  | (13) |
|  |  |  |

Equation (13) shows that the indirect effects are proportional to the direct effects and a second term determined by niche overlap (Fig. 3). As species become more similar in their resource use, approaches one and the strength of the indirect effect increases.  In this case the indirect effect is positive—it amplifies the positive direct effect of the increase in resource supply because we are adding to the resource that is most limiting to the focal species.

*Changes in the non-limiting resource*

Now consider a change in the supply of the resource that is limiting to the competitor. In our example, a small change in *S*2 will not have a direct effect on the focal species, so the net effect must be entirely determined by indirect effects. An increase in *S*2 will have a direct positive effect on the competitor and this will reduce the availability of *R*1 for the focal species. So we can simply solve for net effects as above:

|  |  |  |
| --- | --- | --- |
|  |  | (14) |

We can factor out the definition of niche overlap from the first term on the right hand side and rearrange,

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| --- | --- | --- |
|  |  | (15) |

The sensitivity to the change in *S*2 is similar to the indirect effects of an increase in *S*1 seen in equation (13)—it includes a term that increases as niche overlap approaches one and a term describing how the focal species is affected by the changing resource. Note that the indirect effect is negative, an increase in *S*2 benefits the competitor at the expense of the focal species (Fig. 4). The term gives sensitivity of the focal species to a change in *S*2 in the case that *R*2 is limiting. This should not be confused with the partial derivative which is equal to zero because it is evaluated at the equilibrium where the focal species is not limited by *R*2.

**Substitutable Resource Model**

The essential resource model may not be appropriate for modeling many important competitive interactions, including those among animals competing for shared food resources (Rothhaupt 1988). We extended our analysis to a substitutable resource competition model following Tilman (1982, p. 270):

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| --- | --- | --- |
|  |  | (16) |
|  |  |  |

where *R* is the concentration of each resource, *r* is maximum growth rate of each species, *N* is the biomass or population of each species, *D* is a constant mortality rate, *k* is a half-saturation constant for each species’ use of resources, is a minimum amount of total resource required for growth of each species*,* and *w* is a weighting factor that converts the availability of each resource into its value for each species. Resources are supplied and consumed according to the equations:

|  |  |  |
| --- | --- | --- |
|  |  | (17) |
|  |  |  |

where *S* gives the resource supply point of each resource and *q* gives the amount of each resource consumed per individual of each species. This model assumes a constant diffusion of resources (i.e. the animal prey or plant food) to the consumers. Using a logistic growth function in (17) may be a better way to model biological resources (but see Rothhaupt 1988). Tilman also simplified resource uptake in these equations by assuming that resource uptake is only proportional to consumer abundance: in equation (17), a consumer can continue to draw down resources even when resource availability is infinitesimally small or even negative. This assumption is unrealistic but it should not affect dynamics when considering small changes in resource supply near a positive equilibrium. As in the essential resource model, we will assume that inequality (8) holds: the focal species is limited by *R*1and the competitor is limited by *R*2and the species stably coexist. In Appendix A we show that when these conditions are met niche overlap is defined by the following expression:

|  |  |  |
| --- | --- | --- |
|  |  | (18) |

This definition of niche overlap is more complex than the definition for the essential resource model. In this model niche overlap depends not only on the relative resource consumption rates given by the *q* terms, but also on the relative value of each resource to each species, given by the *w* terms. Barabás et al. (2014) referred to these two aspects of consumer-resource dynamics as the impact niche, given by the *q*’s, and the sensitivity niche, given by the *w*’s.

In order to define net effects, we first solve for the focal species equilibrium abundance and then differentiate with respect to *S*1,

|  |  |  |
| --- | --- | --- |
|  |  | (19) |

These net effects look much like the net effects in the essential resource model. Note that the term on the right resembles the definition of niche overlap, except that it does not include the *w* terms.

Next we solve for the direct effects of a change in *S*1 on the focal species. The steps for doing this are more complicated than in the essential resource model. When both species are competing for resources, the resource concentration equilibrium is where their ZNGI’s intersect. However, when we change the resource supply point, and hold the competitor’s abundance constant at , the resource concentration equilibrium shifts slightly along the focal species ZNGI (Fig. A1). Solving for the direct effects requires that we first solve for the new focal species equilibrium in light of the changing resource supply point and also the shifted resource equilibrium. Doing this we arrive at this expression for direct effects near the equilibrium,

|  |  |  |
| --- | --- | --- |
|  |  | (20) |

The indirect effect is the net effect minus this direct effect,

|  |  |  |
| --- | --- | --- |
|  |  | (21) |

This definition of indirect effects does not include the full definition of niche overlap. Specifically, the relative resource values for the competitor (*w*C1, *w*C2) found in the niche overlap definition in (18) are not found in this equation. In order to see the relationship with the complete expression for niche overlap, we can rewrite this equation in an unsimplified form that does contain the definition of niche overlap,

|  |  |  |
| --- | --- | --- |
|  |  | (22) |

This formula shows that the size and direction of indirect effects depend not only on niche overlap, but also on the difference in direct effects given by the first term in parenthesis on the right-hand-side of equation (22) (see different lines in Fig. 5). By comparison, the essential resource model is a special case of the substitutable resource model where one species is insensitive to the direct effects of a change in resource supply. This is seen by setting the partial derivatives that define direct effects on one or the other species in equation (22) to zero and noting the similarity to equations (13) or (15). At the other extreme, if both species respond equally to the change in the resource (scaled by the term, which is the inverse of the effect of the focal species on the competitor), the indirect effects are equal to zero at all values of niche overlap (line labeled *“0”* in Fig. 5). We confirmed the analytical results for the essential and substitutable models for a limited range of parameters using simulations in the program R (R Core Team, 2014; see zip file provided as supplementary material online).

**Discussion**

The uncertain nature of competition-mediated indirect effects limits our ability to make useful predictions about how anthropogenic change will affect populations and communities. Indirect effects may offset or reverse direct effects and appear an unknown time after direct effects have already been observed (Suttle et al. 2007). We hope to reduce some of the mystery surrounding indirect effects by showing how direct and indirect effects arise in simple mechanistic competition models, and how indirect effect strength can be related to the niche differences that stabilize coexistence between competing species. Consistent with previous work based on phenomenological competition models (Adler et al. 2012), we found that indirect effects were closely related to the stability of coexistence and niche overlap: species that are very similar in their resource requirements are strongly affected by the competition-mediated indirect effects of a change in resource supply points (figs 3,4,5). While it is reassuring that our results are consistent with theory developed in non-mechanistic competition models, our analysis goes a step further by using the recently derived definition of niche overlap from Chesson (2013). Moreover, our use of a mechanistic model that explicitly links environmental change with competition provides novel insights about the strength and direction of indirect effects of environmental change.

Our analysis of an essential resource model shows that a change in resource supply can affect a focal species through two separate pathways: if the resource that is most immediately limiting to the focal species at equilibrium is perturbed, then the focal species is affected by a combination of direct and indirect effects (13), and the magnitude of indirect effects increases with the square of niche overlap (Fig. 3). Alternatively, the focal species can be affected by a change in the supply of the resource that is not immediately limiting to it at equilibrium. In this case, the magnitude of the indirect effect increases with both the niche overlap and the focal species’ sensitivity to the changing resource (eq. [15]; Fig. 4). Indirect effects have their largest magnitude (either positive or negative in sign depending on which resource is perturbed) when niche overlap is high and when the focal species is highly sensitive to the resource that is changing.

Analysis of a substitutable resource model demonstrated that the two distinct modes of indirect effects described above are extremes at either end of a continuum. Indirect effects are strongest when there is a large difference in competing species’ direct sensitivities to the change in resource supply and when niche overlap is large (Fig. 5). In other words, indirect effects require some change in relative fitness between competitors (defined by the difference in direct effects), and this difference is then amplified by the amount of niche overlap. Equation (22) shows that the effect of the focal species on the competitor also matters: when this effect is strong (i.e. small magnitude of), it decreases the magnitude of the competitor’s effect on the focal species.

Competition-mediated indirect effects of a change in resource supply can be summarized as the product of two key components: niche overlap, and the difference between species in direct sensitivities to the change in resource supply (22). In theory, information about direct effects to changes in resource supply should be relatively easy to acquire by studying how species respond to resource manipulation in monoculture (Tilman and Wedin 1991; Adler et al. 2009; Levine et al. 2010). The short-term response of species to an environmental change might also provide information about direct effects (Suttle et al. 2007). Measuring niche overlap is much more data intensive but is possible with a combination of empirical data and models. Chu and Adler (2015) report niche overlap values for 17 pairs of perennial competitors in five different grassland communities and all niche overlap values fell between 0.07 and 0.4. Even in the absence of information about direct effects, these estimates of niche overlap provide information about the maximum magnitude of indirect effects relative to direct effects. Equation (13) shows that niche overlap needs to be above 0.7 for indirect effect strength to equal direct effect strength (Fig. 3); the estimated niche overlap values all fall well below this threshold, meaning that the magnitude of indirect effects would be much less than the magnitude of direct effects. While this simple application of our theory implies that indirect effects might be safely ignored in these communities, it ignores a number of complications. First, Chu and Adler’s niche overlap values are based on a phenomenological approach and undoubtedly reflect more coexistence mechanisms than just resource partitioning (Chesson 2000). Second, pairwise niche overlap values may not be proportional to indirect effects when multiple species are interacting—that is, indirect effects between two species could depend on changes in the abundance of other competitors (Levine 1976). Third, our analysis of competitive interactions does not preclude the possibility of strong indirect effects produced by trophic interactions (Winder and Schindler 2004; Tylianakis et al. 2008; van der Putten et al. 2010; Barton and Ives 2013; Ockendon et al. 2014).

We modeled environmental change as an increase or decrease in the resource supply point. However, there are other ways to model environmental change. We can categorize changes into three groups depending upon their mechanism. In the first group are changes to the environment that cause the resource availability to change, but that leave the species traits that control growth and resource use unchanged. In the second group are environmental perturbations that cause underlying rates of growth and mortality to change. For example, higher temperatures might increase mortality or growth rates (Doak and Morris 2010). Changes in growth or mortality rates will affect equilibrium resource concentrations and species equilibrium abundances but not niche overlap. In the third group are environmental changes that affect the amount of resource taken up per unit of growth, e.g. the *q* or the *w* parameters in equations (9) and (18). Increased atmospheric CO2 for instance, can increase plant water use efficiency (Lee et al. 2001; Reich et al. 2001; Ainsworth and Long 2005), and may also reduce light required for growth (Zotz et al. 2006), while increased temperature may alter nitrogen use efficiency (An et al. 2005) or water use efficiency (Shaw et al. 2000). Similarly, temperature can affect the relative rates at which protists consume different species of bacteria prey, leading to coexistence at some temperatures but competitive exclusion under others (Jiang and Morin 2004). Unlike environmental changes in the first two groups, these kinds of changes affect niche overlap between species and make predicting the outcome of environmental change more difficult. Distinguishing which global change drivers are likely to affect growth and resource use in the three ways outlined here should be a useful first step in categorizing competition-mediated indirect effects.

Our conclusions about the size of indirect effects assume that species can coexist prior to and after anthropogenic change. This assumption is warranted if we are interested in relatively small environmental changes at a short time-scale when colonization and extinction of competitors are unlikely. However, environmental change can rapidly disrupt coexistence in some cases (Jiang and Morin 2004; Stevens et al. 2004; Suttle et al. 2007). In a resource competition model, coexistence requires that the rate of resource supply is greater than the minimum amount required for positive population growth, and also that the ratio of resources supplied falls between the resource use ratios of the focal species and its competitor (see inequality (8) and Fig. 2). A sufficient increase in the supply of one resource can lead to competitive exclusion (Fig. 1; Dybzinski and Tilman 2007). Nevertheless, niche overlap still provides important information: the smaller the niche overlap in terms of resource use ratios, the greater the region of coexistence across a gradient of species performance or resource supply (Barabás et al. 2014). Therefore, changes to resource supply should be less likely to lead to exclusion when niche overlap is small. Moreover, resource partitioning is not the only coexistence mechanism; species-specific responses to spatial heterogeneity, temporal heterogeneity and natural enemies may also contribute to coexistence and further decrease niche overlap (Chesson 2000). Our analysis suggests that management that preserves these mechanisms and keeps niche overlap small could help maintain the diversity of plant and animal communities in the face of anthropogenic changes in resource supply.

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**Online Appendix A: Steps for defining niche overlap for “Indirect effects of environmental change in resource competition models”**

1. **Niche overlap in the essential resource model:**

Chesson (2013) defines niche overlap (eq. [1]) in terms of phenomenological competition coefficients from a two species Lotka-Volterra competition model:

|  |  |  |
| --- | --- | --- |
|  |  | (A1) |
|  |  |  |

Here we use Chesson’s definition to quantify niche overlap in Tilman’s essential resource competition model. To do this, we translate the essential resource model into a Lotka-Volterra competition model. Tilman accomplishes this by rearranging the equilibrium equations for the resource models and finding their algebraic equivalence with a Lotka-Volterra model (Tilman 1982, pp. 190-204). More recently, Meszéna et al. (2006) showed that a mechanistic resource competition model can be translated into a Lotka-Volterra model by linearization of the inter- and intra-specific density dependences at the competitive equilibrium. The linear density dependence of the growth rate of species *i* to the abundance of species *j* at equilibrium is equivalent to the competition coefficients in a Lotka-Volterra model. This provides a valid approximation of a Lotka-Volterra model near the local equilibrium and when resource dynamics are slow relative to population dynamics (Barabás et al. 2013; Meszéna et al. 2006).

In a resource competition model, the growth rate of each species is determined by a vector of sensitivities to each resource, while the impact that a species has on the amount of resources available is determined by a vector of per capita consumption rates. Meszéna et al. (2006) calls these two vectors the sensitivity niche and the impact niche respectively. The competitive effect of species *j* on species *i* at equilibrium is the scalar product of the sensitivity niche of species *i* and the impact niche of species *j*. Thus, if we can calculate the sensitivity of each species’ growth rate to each resource at equilibrium and the per capita impact that each species has on the depletion of each resource we can calculate the Lotka-Volterra equivalents for the resource competition models (see Meszéna et al. (2006) p. 76 for a relevant example).

If we rewrite the resource dependent growth rate of the focal species from equation (6) as:

|  |  |  |
| --- | --- | --- |
|  |  | (A2) |

then the components of the sensitivity vector describing how resource availabilities affect the focal species are . Note that we are concerned with the equilibrium where the focal species is only limited by resource one, therefore the sensitivity to resource two is zero (i.e. ). Likewise, we can define the sensitivity of the competitor and note that at equilibrium its sensitivity to resource one will be zero.

The impact vector for the focal species is defined by how much it depletes resources one and two and is given by setting the equations in (7) to zero and rearranging,

|  |  |
| --- | --- |
|  | (A3) |
|  |  |

where and are introduced to indicate the amount of resource depletion (Meszéna et al. 2006). The components of the impact vectors for each species are then given by the following,

|  |  |
| --- | --- |
|  | (A4) |
|  |  |

The competition coefficients are the products of the resource sensitivities and the per capita impact on the resources,

|  |  |
| --- | --- |
|  | (A5) |
|  |  |

Note that only one resource for each species appears in the above definitions because in this model each species is only sensitive to one resource at equilibrium. When we substitute the mechanistic definitions of the competition coefficients from equation (A5) into Chesson’s definition of niche overlap (Chesson 2013), all the parameters cancel out except for the *q’s* , which define resource consumption rates,

|  |  |  |
| --- | --- | --- |
|  |  | (A6) |

1. **Niche overlap in the substitutable resource model:**

We also derive the Lotka-Volterra competition parameters for a substitutable resource competition model by linearizing the dynamics near the equilibrium (see also Tilman 1982, pp. 270-272). In the substitutable model species are everywhere sensitive to both resources one and two. So the sensitivity niche vector for the focal species will be the partial derivatives of (16) with respect to each resource,

|  |  |
| --- | --- |
|  | (A7) |

The partial derivatives defining the impact niche vectors for the focal species and competitor are found from equations in (17),

|  |  |
| --- | --- |
|  | (A8) |

The scalar product of the sensitivity vectors and the impact vectors give the competition coefficients. For the focal species for example,

|  |  |
| --- | --- |
|  | (A9) |

The same steps can be followed to calculate the competition coefficients for the competitor. These can then be used to define niche overlap for the substitutable model. Note that all the terms but the *q’s* and *w’s* cancel out giving the following,

|  |  |  |
| --- | --- | --- |
|  |  | (A10) |

**References for Appendix A:**

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**Table 1. Symbols used:**

|  |  |
| --- | --- |
| **Variable** | **Definition** |
|  | **direct effect of change in supply of resource *j* on species *i* evaluated near the resource equilibrium** |
|  | **indirect effects of change in supply of resource *j* on species *i*** |
|  | **net effect of a change in supply of resource *j* on species *i*** |
| ***a*** | **resource turnover rate in the essential resource model** |
| ***D*** | **constant mortality rate in the substitutable model** |
| ***kij*** | **amount of resource *j* where population growth rate of species *i* is half of maximum rate** |
| ***m*** | **per capita mortality** |
| ***Ni*** | **population density of species *i*** |
| ***qij*** | **per capita uptake rate of resource *j* by species *i*** |
| ***r*** | **maximum rate of population growth** |
| ***Rj*** | **concentration of resource *j*** |
| ***Sj*** | **resource supply point for resource *j*** |
| ***ij*** | **per capita competition effects of species *j* on species *i*** |
| ****** | **the inverse of the effects of the focal species on the competitor** |
| ****** | **niche overlap** |
| ***i*** | **the minimum amount of total resource required for growth of species *i* in the substitutable model.** |
| ***wij*** | **a weighting factor that converts the availability of each resource *j* into its value for each species *i* in the substitutable model.** |

**Figure legends:**

Figure 1: The hypothetical change in focal species abundance (*N*F\*) caused by environmental change. When competitive interactions are allowed to change, the focal species abundance increases along with environmental change (“net effect”, dashed line). When competitive interactions are held constant at the initial level, the focal species abundance increases less steeply as the environment changes (“direct effect”, solid line). The indirect effect is the difference between the slopes of the direct and net effects. In this example the indirect effect amplifies the positive direct effect. To the right of the dotted vertical line the focal species excludes its competitor and there are no competition-mediated indirect effects. Our analysis focuses on indirect effects in the region of parameter space where the focal species and its competitors can stably coexist—left of the dotted line. The inset shows how an environmental driver affects the focal species directly (arrow a) and indirectly by changes in competitive interactions (arrows b and c).

Figure 2: A ZNGI plot for two species competing for two essential resources. The resource consumption vectors for the focal species and competitor are given by the values in parentheses and shown with the dashed black and gray lines. Coexistence is possible when the resource supply point (*S*1, *S*2) falls between the two resource consumption vectors. The niche overlap between species, , will generally decrease as the angle between the resource consumption vectors increases. In this example niche overlap would be equal to 0.41 using equation (9).

Figure 3: Competition-mediated indirect effects on the focal species when there is a change in the supply point of the essential resource (*S*1) limiting the focal species. The indirect effects depend on both niche overlap and the direct effect of the change in resource supply point, . These figures present two different ways of looking at indirect effects: in A) niche overlap is on the x-axis with different lines for three different sensitivities to direct effects. In B) focal sensitivity to direct effects is on the x-axis with different lines for three different values of niche overlap.

Figure 4: Competition-mediated indirect effects on the focal species when there is a change in the supply point for the essential resource limiting to its competitor (*S*2). The effects depend on niche overlap () and the sensitivity of the focal species to the changing resource, . A) Niche overlap is shown on the x-axis with different lines for three different values of focal species’ sensitivity to *S*2. B) The focal species’ direct sensitivity to *S*2 is on the x-axis and different lines are shown for three different values of niche overlap.

Figure 5: Indirect effects of a change in resource supply point in a substitutable resource model. Indirect effects on the focal species increase with niche overlap (), but also depend on each species’ direct sensitivity to the change in resource supply (see equation [22]). Numbers next to each line give the difference between the focal species’ and competitor’s direct sensitivities to a change in resource supply. The indirect effects are positive when the focal species’ sensitivity to direct effects is greater than the competitor’s, and negative when the focal species’ sensitivity is less than the competitor’s. All lines are calculated with in equation (22).

Figure A1: A ZNGI plot for two species competing for two substitutable resources. The resource consumption vectors for the focal species and competitor are given by the values in parenthesis and shown with the dashed black and gray lines. Coexistence is possible when the resource supply point (*S*1, *S*2) falls between the two resource consumption vectors. The equilibrium resource concentration is found at . However, when defining direct effects on the focal species, the resource supply point is shifted (new ) but the competitor’s abundance is held constant; in this case the equilibrium resource concentration will shift slightly along the focal species ZNGI (new . This shift needs to be taken into account when solving for focal species’ direct sensitivity to a change in the resource environment.

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