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The consequences of multiple indirect pathways of interaction for species coexistence

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Abstract Species in diverse communities typically have direct interactions with a small subset of other species, yet indirect effects can be traced between all of the species in a community. When multiple pathways of indirect effects link a pair of species, the magnitude and sign of the net effects depend on the details of the links in each indirect pathway. We explore the effects of alternative indirect pathways in a food web module that includes predation, competition, and mutualistic interactions; mutualisms are an important component of natural interaction networks, but are underrepresented in theoretical studies of indirect interactions. We use a conjugate variable method to partition the strength of a net indirect effect between two species that do not directly interact into two partial effects transmitted along two separate but simultaneously acting pathways: a pathway mediated by a shared predator and a pathway mediated by competing resources. Though the sign of each partial effect is generally negative, as expected, the strengths of the partial effects are different than if they occurred in isolation of one another. Summing the purely predator-mediated indirect effect and the purely resource-mediated indirect effect does not yield the net effect when they occur together. We find that when a resource-mediated pathway for an indirect effect is present, the presence of a shared predator can facilitate coexistence between apparent competitors, even allowing for the persistence of the species more vulnerable to predation. This approach holds promise for building a better understanding of the ways that indirect effects propagate through communities to affect patterns of relative abundance and coexistence.

Keywords Apparent competition · Food web module · Indirect effects · Interaction strength · Mutualism · Network · Predation · Resource competition

Introduction

Communities are dependent on interspecific interactions that play out within ecological networks. The architecture of a network is formed of pairwise direct interactions, such as predation, competition, and mutualism. But species can also interact indirectly via one or more intermediaries (reviewed in Wootton 1994). Though many species do not interact directly, indirect effects permeate ecological networks, linking the dynamics of all species in a community. Accordingly, the strength of indirect effects can have important consequences for patterns of diversity and species coexistence (Higashi and Patten 1989; Menge 1995; Borrett et al. 2010). Moreover, ecological networks are complex and tend to have architectures that lead to more than one indirect pathway between pairs (Higashi and Nakajima 1995; Yodzis 2000). Developing an understanding of how indirect effects are partitioned among multiple and simultaneously acting pathways is important for understanding mechanisms of coexistence. For example, attributing an indirect effect to a single pathway, when multiple pathways are operating, may lead to simplistic or even erroneous conclusions about the nature of indirect interactions between species.

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Apparent competition is a well-known example of negative indirect interaction (Holt 1977) and can be an important driver of community structure (e.g., Bonsall and Hassell 1997; Morris et al. 2004). A shared predator can link the dynamics of two species that do not directly interact: an increase in the density of one species allows the predator population to increase and thus prey more heavily on the other (reviewed in van Veen et al. 2006). If the predator was not considered, the negative response of one species to the presence of other would give the (false) appearance of interspecific competition. Such a negative indirect effect could also be transmitted along other pathways (Connell 1990), yet few of the alternative pathways have been explored, either empirically or theoretically.

A negative indirect effect may also pass through a lower trophic level. The conceptual model in Fig. 1 illustrates a community module that can exhibit both apparent competition mediated by a shared predator and a reciprocal negative indirect effect transmitted via a lower trophic level. For example, the two species M_i could represent specialist pollinators, such as solitary bees, both preyed upon by species P, such as a parasitoid that can attack multiple hosts or a generalist predator such as a robber fly (Asilidae) or crab spider (e.g., Thomisidae). The partners for each of the specialist pollinators are their respective plant resources (R_i), which are assumed to have interspecific competition. If pollination by one bee species (M_1) results in an increase in its mutualist plant's (R_1) density, the net interspecific competition between the two plant species will also increase, thereby reducing the density of the other plant species (R_2). If it is at a lower density, the competitor (R_2) will be less capable of providing benefit to its own specialist mutualist (M_2) and vice versa. Thus, there is a reciprocal negative indirect effect between the two pollinator species (M_1 and M_2), which do not directly interact. This reciprocal negative indirect effect, in contrast to classic apparent competition, is transmitted via a combination of mutualisms and interspecific competition between resource species (R_1 and R_2). To the extent that the fundamental feature of apparent competition is that two species resemble competitors because of a negative indirect effect, the indirect interactions between M_1 and M_2 can be described as both predator- and resource-mediated apparent competition. In even moderately diverse communities, these effects along with other types of indirect effects transmitted via pathways with multiple species are likely to occur simultaneously.

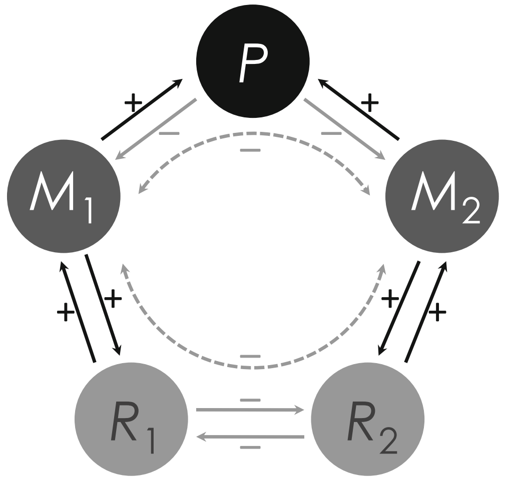


Fig. 1 Interaction network depicting the sign of the direct effects between species (*solid arrows*) and the hypothesized partial indirect effects between M_1 and M_2 mediated by a shared predator (*upper dashed arrow*) and competing resources (*lower dashed arrow*). Positive and negative effects are indicated by *black* and *gray lines*, respectively

A predator generally has a negative effect on the abundance of its prey and, in the absence of other regulating factors, will result in the exclusion of the prey species most vulnerable to predation (the weaker apparent competitor; Holt 1984). If predator- and resource-mediated pathways of apparent competition are acting in concert, one might predict a combined negative effect that would hasten the extinction of the weaker apparent competitor. However, predation is known to promote coexistence in some systems where resource competition would otherwise result in the exclusion of an inferior competitor (Paine 1966; Caswell 1978; Inouye et al. 1980). A predator may promote coexistence by acting to stabilize the dynamics of its prey (reviewed in Chesson 2000). For example, a shared predator may reduce population sizes and therefore moderate the strength of interactions between prey species that occur via other pathways (Chase et al. 2002). Thus, a shared predator may have effects on the relationship between species in the presence of multiple interaction pathways that could not be predicted based on the outcome of interactions along a single pathway.

The ecological networks of real communities, where competition, predation, and mutualism can happen simultaneously, are highly complex. We therefore explore a simple interaction web that combines these three types of direct interactions (Fig. 1). We will focus on the two species at an intermediate trophic level. These species interact only indirectly but via two different and simultaneously acting pathways: resource- and predator-mediated pathways. We use the inverse of the community matrix to quantify the strength of interactions in order to examine the resulting effects on species coexistence. We then apply a rarely used approach developed by Nakajima and Higashi (1995) to evaluate the partial effect propagated along a particular pathway when multiple pathways are acting simultaneously. In addition, the quality of service provided to a mutualist partner can vary among species (Schemske and Horvitz 1984; Francis and Read 1995; Miller 2007) or over time within species (e.g., Grinath et al. 2012), so the strength of mutualism may play an important role in determining a species' abundance or persistence. Thus, we also investigate how indirect effects are influenced by the strength of mutualistic benefit that the intermediate trophic level provides to resource species, and whether this changes in different competitive and predation environments.

Model description

The community in our model is comprised of five species in three trophic levels: a generalist predator (P), two prey species (M_1 and M_2), and two species at a lower trophic level (R_1 and R_2). Each of the prey species has a specialized mutualism with its sole resource (R_1 or R_2), and the resource species engage in interspecific competition (Fig. 1). As described above, this food web module may be thought of as a plant-pollinator system where specialist pollinators are preyed upon by a generalist crab spider; however, many other ecological systems could fit within our model framework. We use a system of differential equations modified from the commonly used Lotka-Volterra competition and predation models to describe population dynamics in the five-species community. Because the interaction network is symmetric, we show equations for R_i and M_i, where $i=1$ when $j=2$ and $i=2$ when $j=1$.

$$\frac{dR_i}{dt}=r_iR_i\left(1-\frac{R_i+R_j\alpha_{ij}}{K_i+\gamma_iM_i\left(\frac{s_iR_i}{1+s_ih_iR_i}\right)}\right) \tag{1}$$

$$\frac{dM_i}{dt}=b_iM_i\left(\frac{s_iR_i}{1+s_ih_iR_i}\right)-d_iM_i(1+e_iM_i)-\frac{c_iM_iP}{1+c_if_iM_i} \tag{2}$$

$$\frac{dP}{dt}=P\left(\frac{v_1c_1M_1+v_2c_2M_2}{1+c_1f_1M_1+c_2f_2M_2}\right)-mP \tag{3}$$

For the lowest trophic level, R_i (Eq. 1), r_i is the intrinsic rate of growth, K_i is the single-species carrying capacity, and α_{ij} is the per capita competitive effect of R_j on R_i. γ_i determines the strength of the benefit to population growth that M_i provides to R_i. As this benefit enhances R_i carrying capacity, we therefore assume that in the absence of competitors, R_i is not dependent on M_i for persistence and that M_i provides a service (e.g., pollination) that allows R_i to persist at a greater equilibrium density.

We treat the mutualism between M_i and R_i as a consumer-resource interaction (Holland et al. 2005; Holland and DeAngelis 2010). The obligate mutualist M_i converts resources provided by R_i to new growth at a rate b_i, while suffering density-dependent (e_i) and density-independent mortality (d_i) (Eq. 2). Incorporating density-dependent mortality in this way (Neuhauser and Fargione 2004) allows for stable coexistence of mutualistic partners by preventing unbounded growth (May 1981). We use a saturating (type II; Holling 1959) functional response to describe beneficial interactions between M_i and R_i, where h_i is the handling time, which helps determine the asymptotic saturating benefit of the mutualism, and s_i is the encounter rate, which determines the rate of saturation. The benefit that a mutualist provides its partner often saturates as pollinators, for example, have a finite ability to find and process floral rewards (e.g., Morris et al. 2010). A saturating functional response is therefore often used to model mutualistic interactions (e.g., Holland et al. 2002; Feldman et al. 2004; Zhang et al. 2011). Though γ_i is a measure of the beneficial effect of M_i on R_i, increasing γ_i has a reciprocal benefit for M_i in the form of a larger population of its sole resource. We therefore refer to γ_i as the strength of mutualism between M_i and R_i.

The predator, P, preys on M_1 and M_2, converting prey to population growth at a rate v_i (Eq. 3). As above, we use a saturating response, assuming that the predator has a finite ability to capture and process prey, where c_i is the capture rate and f_i is the handling time.

Model analysis

The community matrix (Jacobian), **A**, represents the set of all direct pairwise interactions between species in a community (Levins 1968; Vandermeer 1970). The elements of **A** are $A_{ij}=(dN_i/dt)/\partial N_j$, with all species N evaluated at equilibrium, i.e., the partial derivative A_{ij} denotes the direct effect of a change in density of species j on the equilibrium density of species i, with other species in the network held constant. In the absence of a direct interaction between two species $A_{ij}=0$. The negative inverse of the community matrix, $-(\mathbf{A}^{-1})$, yields the net interaction coefficients of all species in the community (Levine 1976; Bender et al. 1984; Stone and Roberts 1991; Schmitz 1997). Net interaction coefficients represent the sum of direct and indirect interactions, through all possible pathways, between each species pair in the community, evaluated at equilibrium. The net indirect effect of any species on another is thus the difference between the entries of **A** and $-(\mathbf{A}^{-1})$. Because there is no direct interaction between M_1 and M_2, the net effect is purely indirect and reciprocal negative values represent apparent competition.

We partition two simultaneously acting pathways of indirect effects using the conjugate variable approach, which was developed by Nakajima and Higashi (1995) and then independently by Yodzis (2000). The partial effect of species j on species i that passes through species k is given by

$$a_{ij,k}=\frac{a_{ik}a_{kj}}{a_{kk}} \tag{4}$$

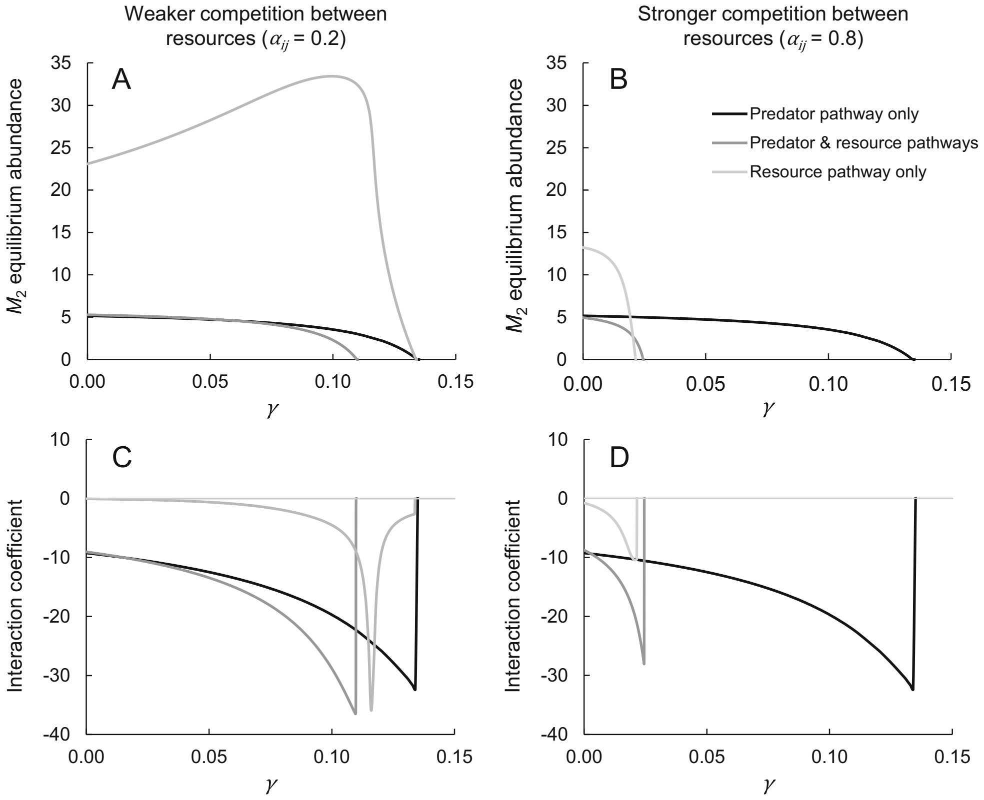
where a_{ij} are elements of -($\mathbf{A}^{-1}$). The remainder of the net effect, which does not pass through species i, is equal to $a_{ij} - a_{ij,k}$. The conjugate variable approach is used to quantify the role of a particular species (k) in mediating a net effect between two others (i and j). Because there is only one species (the predator, P) between M_1 and M_2 along the predation pathway, we interpret $a_{M_iM_j,P}$ as the portion of the total indirect effect that is transmitted along this pathway. Further, we interpret the difference between the net effect and $a_{M_iM_j,P}$ as the partial indirect effect transferred along the resource pathway.

We analyzed the strength of the indirect effect of M_1 on M_2 across a range of strengths of mutualistic benefit (γ_i, Eq. 1) provided by M_i to R_i in different predation and competitive environments. To assess the roles of the two indirect pathways in the strength of the total indirect effect, most parameter values for M_1 and M_2 and for R_1 and R_2 were made symmetrical, except that M_1 was given a slight advantage in γ (+0.01) and c (−0.005) in order to avoid a singularity in the inverse community matrix (see the legend of Fig. 2 for parameter values). To assess the effect of γ and multiple indirect pathways of interaction on species coexistence, we modeled asymmetric mutualism strengths across γ values from 0 to 0.15 in different predation and competitive environments. Our model was implemented in R v3.1.1 (R Development Core Team 2014). We used the runsteady function in the R package rootSolve (Soetaert and Herman 2009) to determine equilibrium densities. A species was considered extinct if its equilibrium density was below 10^{-4}. We examined a range of starting conditions and though our search was not exhaustive, we found no evidence of alternative stable states. Simulations of community dynamics showed that damped cycles can occur but the system settles to a stable equilibrium (Supplementary material), where our analysis of indirect effects is applied.

Results and discussion

Indirect effects following alternative pathways have different and unexpected effects on equilibria and persistence in ecological communities. We first discuss the effects of the different forms of interaction on the equilibrium abundance and coexistence of species and then discuss the importance of net and partial indirect effects for coexistence, focusing on the persistence of M_2.

The mutualists M_i and R_i increase each other's equilibrium population sizes through an exchange of benefits, and in isolation from other species, equilibrium population sizes increase with the strength mutualism (γ; results not shown). Competition between the resources (R_1 and R_2) of the two mutualistic pairs can affect the equilibrium abundances of each of these four species. For example, when competition



Weaker competition between resources (α_{ij} = 0.2)

Stronger competition between resources (α_{ij} = 0.8)

Fig. 2 The equilibrium abundance of M_2 (**a** and **b**) and the strength of the total indirect effect of M_1 on M_2 (**c** and **d**) varies with the benefit M_i provides to R_i (γ_i) and which pathway(s) of the indirect effect are present (*different line shades*). The x-axis, γ, is the value of γ_2; γ_1=γ_2+0.01. Results are shown for weaker competition (α_{ij}=0.2; **a** and **c**) and stronger competition (α_{ij}=0.8; **b** and **d**) when competition between R_1 and R_2 is present in the food web module. The results representing the effects of the predator-mediated pathway only (i.e., when competition between R_1 and R_2 is absent and α_{ij}=0) are shown by the *black lines*; these are identical across panels **a**, **b** and **c**, **d** but are shown in both for reference. Other parameter values: r_i=1.0, K_i=10, b_i=0.2, s_i=0.3, h_i=0.2, d_i=0.1, e_i= 0.1, v_i=0.1, c_2=0.1, c_1=c_2 − 0.005, f_i=0.1, m=0.1

is low (α_{ij}=0.2), the equilibrium abundance of M_2 increases with γ throughout most of the range of γ in which all species coexist (light gray line in Fig. 2a). However, because M_1 has a slight advantage in the strength of mutualism (γ_1=γ_2+0.01), a parallel increase in the γ_i values eventually results in the exclusion of M_2 at sufficiently high levels of γ_i due to the reduced density of its mutualistic partner, R_2. M_1 always provides a slightly greater benefit to its partner R_1 than M_2 does to R_2, and after a point, the increasing competitive effects of R_1 on R_2 outweigh the benefits to R_2 of a higher γ. When per capita competition is stronger (e.g., when α_{ij}=0.8), parallel increases in γ_i only decrease the equilibrium abundance of M_2 (light gray line in Fig. 2b), because increases in γ_i at this level of competition are not sufficient to counter the increasingly negative competitive effects of R_1 on R_2.

The presence of a shared predator, P, usually results in lower equilibrium abundances of M_2 as compared to communities where the predator is absent (Fig. 2a, b). This is a result of the direct effect of predation and the familiar indirect effect of apparent competition. With a shared predator, a parallel increase in γ_1 and γ_2 results in decreased equilibrium abundances for M_2 across the entire range of γ values for which species coexist. For the range of parameter values we explored, this is the case whether or not a resource-mediated pathway is present.

Net indirect effects

The sign of the indirect effect of M_1 on M_2 (and vice versa) is negative across the range of parameter values explored here (Fig. 2c, d). Because M_1 and M_2 do not interact directly or compete for a shared resource, i.e., resource competition, we consider this to be a form of apparent competition mediated by two different pathways: predator- and resource-mediated pathways.

A combined negative effect of these two pathways might be expected, such that the exclusion of the weaker apparent competitor would be hastened when both pathways simultaneously transmit a negative indirect effect. This does occur when competition is relatively weak; M_2 persists over a smaller range of γ when both pathways are present compared to when only the resource-mediated pathway is present (compare light and dark gray lines in Fig. 2a). However, when competition between resources is stronger, shared predation instead extends the range of γ for which M_1 and M_2 coexist (compare light and dark gray lines in Fig. 2b), illustrating how the single-pathway effects may not combine as expected. In the case with stronger competition between resource species (R_i), the inferior apparent competitor (M_2) persists over a wider range of parameter space in the presence of a shared predator, even though it is attacked by the predator at a slightly greater rate (recall $c_1<c_2$, in order to avoid a singularity in the inverse Jacobian). The greater range of coexistence may be a result of opposing direct and indirect effects of the predator on M_2. The indirect positive effect of the predator on M_2 is seen by multiplying the signs of interactions counter-clockwise around the diagram in Fig. 1. Predation on M_1 (usually the source of predator-mediated apparent competition with M_2) means M_1 provides less benefit to its partner, R_1, resulting in reduced competition with R_2. Greater R_2 density then increases M_2 density: an indirect positive effect of the predator on M_2. As γ_i increases, the *negative direct* effect of the P on M_2 is increasingly countered by the *positive indirect* effect. This is shown in Fig. 3, where the net effect of the predator on M_2 diminishes and even becomes positive over a narrow range of γ values. Therefore, even though the shared predator can intensify net indirect interactions between M_1 and M_2 (Fig. 2), the predator can mediate coexistence through a counteracting stabilizing effect, which increases biodiversity by allowing all species in a community to persist over a broader range of ecological conditions.

When both pathways of apparent competition are acting simultaneously and γ_1 and γ_2 are varied independently, the strength of predation and the strength of competition between resources (both of which should affect M_1 and M_2 negatively) affect coexistence of M_1 and M_2 differently (Fig. 4). With predation rates fixed (c_i and c_j=0.09), the range of γ_i over which apparent competitors coexist *decreases* with the strength of competition (α_{ij}) between their resources (Fig. 4a). Conversely, when the strength of competition is fixed (α_{ij} and α_{ji}=0.6), the range of γ_i over which M_1 and M_2 coexist *increases* with the strength of predation (Fig. 4), again demonstrating that the different pathways contribute uniquely to community dynamics. However, similar to the results shown in Fig. 2a, when competition between resources is sufficiently low (e.g., α_{ji}=0.2), increasing the strength of

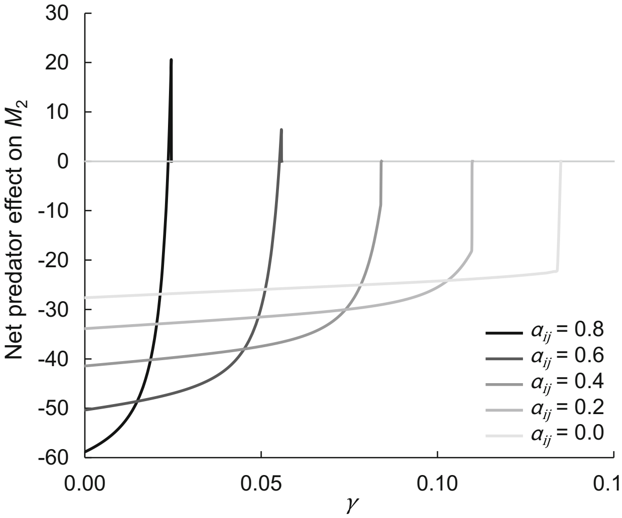


Fig. 3 Net effect of the predator P on M_2 (a_{M_2P} from $-(\mathbf{A}^{-1})$) for a range of mutualism strength (the x-axis, γ, is the value of γ_2; γ_1=γ_2+0.01.), resource competition strength, and fixed capture rate (c_1=0.09, c_2=0.095). Other parameter values are the same as indicated in Fig. 2

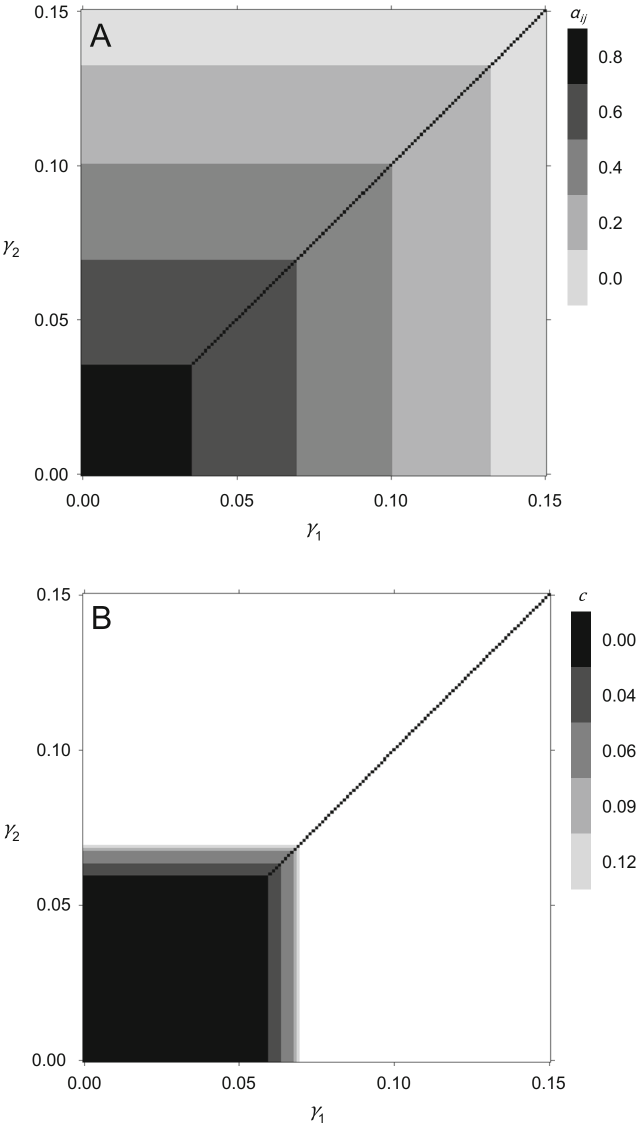


Fig. 4 Coexistence of M_1 and M_2 across a range of γ_1 and γ_2 in different competitive (**a**) and predation (**b**) environments. *Shaded areas* indicate coexistence and *darker shades* overlap areas of *lighter shades*. **a** Increasing the strength of competition between resources decreases the area of coexistence. At a fixed capture rate (c_1=c_2=0.09), the area of coexistence is greatest when competition is relatively weak, and the area of coexistence decreases as the strength of competition between resources increases. **b** Increasing the capture rate increases the area of coexistence (c_1=c_2). For a fixed level of competition (α_{ij}=0.6), increasing the capture rate allows for coexistence across a greater range of parameter space. Parameter values are the same as given in Fig. 2 except where noted. In **a** and **b**, M_1 always persists below the diagonal, and M_2 always persists above the diagonal

predation can decrease the range of coexistence (results not shown). Moreover, the presence of an indirect pathway through the upper trophic level can, to a degree, provide for coexistence over a greater range of parameter values. Again, this is counter to what would be expected if partial indirect effects combine as if they were acting alone.

Partitioning the indirect effect of M_1 on M_2 between predator and resource pathways

In order to understand how the indirect effect between M_1 and M_2 is propagated through simultaneously acting pathways, we partitioned the indirect effect between the predator and resource pathways using the conjugate variable approach (Nakajima and Higashi 1995; Fig. 5). As the strength of γ_i increases, the proportional contributions of the two pathways to the total indirect effect changes. At low values of γ_i, the net effect is dominated by the predator pathway, but as γ_i increases there is a switch to domination by the pathway mediated by the competing resources. The magnitude of the partial effect transmitted through the resources appears to depend more strongly on the strength of the mutualism than does the partial effect transmitted through the predator. Moreover, when competition between resources is weaker (α_{ij}=0.2), the partial effect mediated by the predator is dominant over much of the range of γ_i we investigated. However, when competition is stronger (α_{ij}=0.8), the partial effect mediated by the resource species is dominant over a greater proportion of this range of γ_i. This switch in the relative importance of the two pathways as γ_i gets large likely occurs because of the importance of the strength of mutualism for determining the net strength of competition between R_1 and R_2, and hence the beneficial effect of R_i on M_i. By comparison, the strength of mutualism between M_i and R_i has little effect on M_i predation.

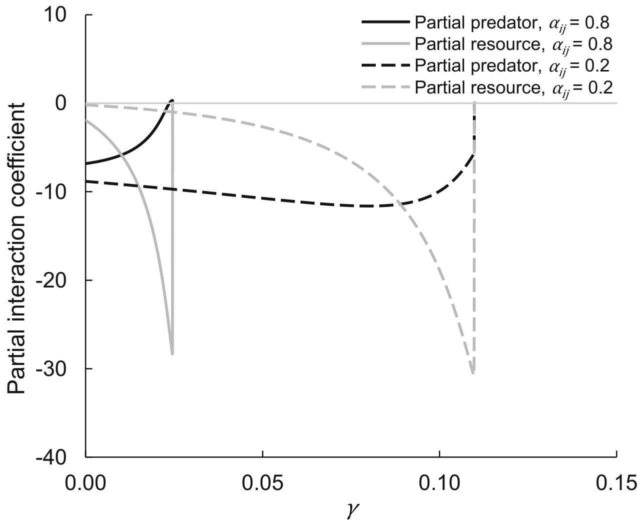


Fig. 5 The net indirect effect of M_1 on M_2 partitioned between simultaneously acting pathways across a gradient in mutualism strength (the x-axis, γ, is the value of γ_2; γ_1=γ_2+0.01.). The partial strengths of the effect transmitted through the predator (*black*) and resource (*gray*) pathways are shown for weaker (*dashed line*; α_{ij}=0.2) and stronger (*solid line*; α_{ij}=0.8) per capita competition between resources. Summing the two *dashed* or two *solid lines*, respectively, equal the net indirect effect of M_1 on M_2 as depicted by the medium *gray lines* in Fig. 2c, d. Parameter values are the same as for Fig. 2

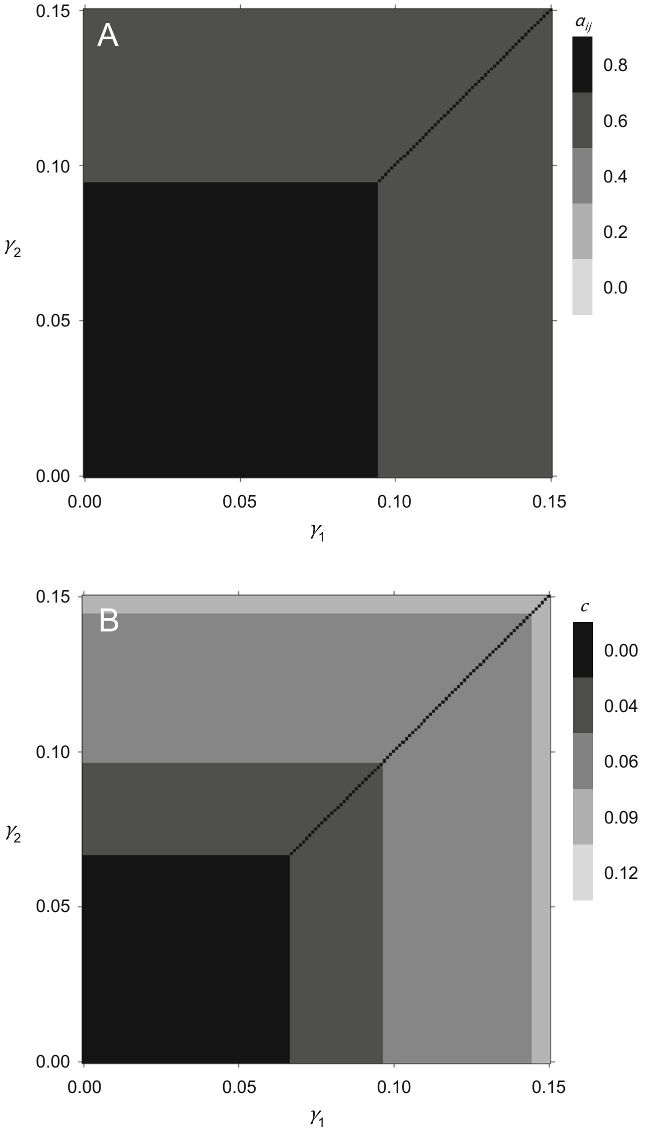


Fig. 6 Coexistence of R_1 and R_2 across a range of γ_1 and γ_2 in different competitive environments (**a**) and capture rates of M_1 and M_2 (**b**). Areas of coexistence represented by *lighter shades* are included in the *darker shaded areas*. **a** At a fixed capture rate ($c_1=c_2=0.09$), R_1 and R_2 coexist across the range of γ modeled except for when competition is strongest ($\alpha_{ij}=0.8$). **b** Increasing the capture rate of the mutualist partners of R_1 and R_2 has the opposite effect ($c_1=c_2$). For a fixed level of competition ($\alpha_{ij}=0.6$), increasing the capture rate allows for coexistence across a greater range of parameter space. Parameter values are the same as given in Fig. 2 except where noted. In **a** and **b**, R_1 persists below the diagonal, and R_2 persists above the diagonal

Mutualism effects on the broader community

Mutualists confer important benefits on their partners (reviewed in Boucher et al. 1982) that likely affect the way their partners interact with other species in a community. The quality of service can vary among alternative mutualist species (Schemske and Horvitz 1984; Palmer et al. 2010; Bruna et al. 2014) and vary spatially or temporally within species (Grinath et al. 2012). Thus, not only is the presence of a mutualism important but the quality of beneficial services is likely also important for mediating interactions with other species in a community. Our results suggest that the level of benefit a mutualistic species confers on its partner can have important consequences for the community at large. Even with no direct interactions between them, the provision of mutualistic benefits (magnitude of γ) can determine whether M_1 and M_2 coexist (Fig. 4). In Fig. 4, M_1 always persists below the diagonal, and M_2 always persists above the diagonal. The vertical and horizontal boundaries to coexistence in Fig. 4 indicate that there is a threshold level of γ above which coexistence is impossible and only the species with the larger value of γ will persist. For example, as γ_1 increases and M_2 nears zero as it approaches its persistence barrier, γ_2 will have little effect on M_2. That is, when M_2 is at low density near its boundary to persistence, it will provide little benefit to R_2 and hence receive little reciprocal benefit to its own population growth. Therefore, if γ_1 is above its threshold, increasing γ_2 will yield no extra benefit for R_2 and cannot allow M_2 to persist until γ_2 increases to greater than γ_1. Moreover, although we focus on M_1 and M_2 here, changes in the quality of service provided by a mutualistic partner (γ) can also alter the outcome of competitive interactions and coexistence with other species in the community (e.g., R_1 and R_2 in Fig. 6). The vertical and horizontal boundaries for coexistence of R_1 and R_2 in Fig. 6 are a result of similar processes. M_2 cannot persist in the area of parameter space near the R_2 persistence boundary and thus R_2 receives no extra benefit from an increase in γ_2.

Conclusions

Indirect effects can follow multiple pathways and result in diverse outcomes for relative abundance and coexistence, even in a relatively simple five-species community. A resource-mediated pathway for a negative indirect effect between species at an intermediate trophic level can mimic the effects of a predator-mediated pathway (i.e., apparent competition). The presence of both resource- and predator-mediated pathways can allow for coexistence over a greater range of parameter space than when only the resource-mediated pathway is present. However, the effect of multiple indirect pathways in a dynamic system is not the combination of indirect interactions acting in isolation of other pathways. Understanding multiple simultaneous mechanisms of apparent competition is important for explaining how each pathway contributes to observed community dynamics. For example, empirical studies of only the predator pathway, when multiple indirect pathways are in fact operating, may overestimate a predator's contribution to the indirect negative effect between species.

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