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Trait and density mediated indirect interactions in simple food webs

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This article compares indirect trait-mediated interactions in simple resource–consumer–predator food webs with those that are density-mediated. It focuses on two well documented responses of consumers to predation risk: decrease in consumer activity and habitat switch. These behavioral effects are transmitted to resources and they cause similar indirect effects as those which are mediated by density changes in consumers. Two indirect interactions are studied in this article: trophic cascades, and apparent competition. Results for density only, trait only and combined density and trait mediated interactions are compared and discussed with respect to manipulation with predator density (top-down manipulation) and resource environmental capacity (bottom-up manipulation). The article shows that trait-mediated, effects on species equilibrial densities are similar to those of density-mediated, but they are often highly non-linear. Thus, they may have potential for even stronger impact on food webs than those which are density mediated.

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In community ecology, the ability to predict reliably the effects of species interactions on community dynamics hinges on understanding and characterizing two fundamentally important properties: (1) the nature and strength of emergent indirect effects; and (2) the way organizational hierarchies (e.g. individual, population, and community) are dynamically linked. The imperative to understand the nature and strength of emergent indirect effects comes from realizing that simply summing the effects of all pair-wise interactions along chains of species that are dynamically coupled may be insufficient to predict community dynamics. This is because indirect effects have the potential to swamp out the direct effects (Yodzis 1988, Schoener 1993, Menge 1995, Abrams et al. 1996, McCann et al. 1998). The need to consider organizational hierarchies derives from the recognition that classical approaches, which characterize interactions wholly in terms of population density, may incorrectly assume that it is sufficient to abstract lower individual-scale mechanistic details as model parameters (e.g. consumer foraging behavior subsumed in a cropping rate parameter of the functional response). It is implied, in such constructs, that the parameters do not change over the time scale of population dynamics. However, if individual-scale details cause the parameters to vary on the same time scale as changes in population density then one must account for the effects of lower-scale detail on dynamics (Abrams 1995, Peckarsky et al. 1997).

For example, in natural systems predators can influence the abundance of prey by direct and indirect means that transcend two organizational hierarchies. They directly kill prey by capturing and consuming them. They indirectly kill prey by causing them to alter their foraging behavior in response to the mere presence of the predators risk effects (e.g. seeking refuge or becoming

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vigilant at the expense of feeding). Altered foraging can result in increased risk of starvation relative to conditions without predators (McNamara and Houston 1987, 1996) which also causes reduction in prey density. The critical issue here, when attempting to derive an understanding of population and community dynamics using empirical research programs, is that the trait-mediated effects will remain masked if we measure net effects of predators simply as density responses of prey. Thus, "unmasking" the amount of variation in prey density that is attributable to trait-mediated effects requires that we conduct field experiments in ways that differ from those that would be motivated by classical "predation-mediated" theory that abstracts lower-scale detail. Specifically, field experiments must be designed not only to manipulate predator density but also to switch "on and off" the act of direct predation. One then compares the effects of predator presence alone (risk effects) on population and community dynamics relative to effects of risk and predation operating simultaneously (Schmitz et al. 1997, Peacor and Werner 2001).

Our purpose here is to motivate new kinds of field research that quantifies the contribution of trait-mediated and predation-mediated effects on population dynamics. We present a collection of models that are caricatures of simple food webs. We use these to illustrate the principles involved in transmission of direct and indirect effects across organizational hierarchies. We show that trait-mediated effects can have quantitatively important consequences to food web dynamics and that these consequences are often qualitatively similar to those mediated through density changes in intervening species due to predation. Our point here is to show that if experiments are not designed to separate out trait-mediated and predation-mediated effects on dynamics, community ecologists may continue to surmise incorrectly that the important causal driver of food web dynamics is predation (i.e. killing a prey by its predator).

We use two community modules (Holt 1995) that form the conceptual foundation for understanding direct and indirect effects in community ecology (Polis 1991, 1994, Strong 1992, Holt 1995, Polis and Strong 1996, Huxel and McCann 1998, McCann et al. 1998). The first module is the widely celebrated example of indirect effects that emerge when species of top predators influence the abundance of species in non-adjacent lower levels of food webs through direct interactions with their prey species – called a trophic cascade. The second module involves interactions that occur when two resources, that do not interact directly (for example they may be spatially segregated) interact indirectly because they share a consumer – called apparent competition (Holt 1977, 1984, 1995). In such a case, one resource species can be eliminated from a community by the other species by way of enhancing the population abundance or persistence of the shared predator.

Model systems

We conceptualize model ecological communities simply as a collection of consumers of resources that themselves are resources for higher-level consumers. This reasoning enables us to assemble a community, in theory, by connecting pair-wise consumer–resource systems to create food webs with different topologies (Fig. 1). Each link in this chain will have a different nature depending on the kinds of consumers and resources involved, e.g. plant–soil nutrients, herbivore–plant, carnivore–herbivore. We also assume that similar consumer species (e.g. herbivores) can be assigned to the same trophic level in the web because they have the same effect on resources. These conceptions of communities obviously ignore the range of direct interactions that occur laterally within trophic levels of food chains (e.g. interspecific competition, mutualism, intraguild predation) and across multiple trophic levels (e.g. omnivory). So, we recognize that our minimalist constructs will not capture the breadth of biological interactions that could occur in natural systems (Leibold 1996, Polis and Strong 1996, McCann et a1. 1998). The reason we make these simplifying assumptions, however, is that they allow us to develop the kind of theoretical framework needed to illustrate that complex nature of interactions and dynamics that derive from the interplay between individual-scale and population-scale phenomena independently of complexities that arise simply because species occur in highly interconnected networks of direct and indirect interactions.

Trophic cascades in linear food chains

We begin with the most basic conceptualization of a food web, a linear chain comprised of two consumer–resource links, that between a herbivore and plant and that between a carnivore and a herbivore. In principle,

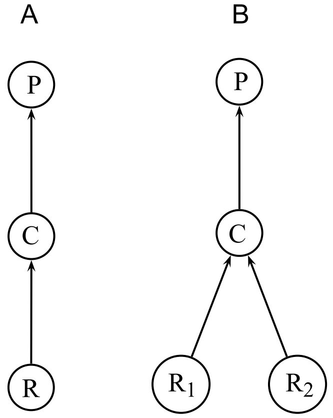

Fig. 1. Food web topologies. (A) food chain, (B) food web with two resources.

this conception led to the well-known body of theory describing tri-trophic interactions in communities of plants, herbivores and carnivores (Rosenzweig 1973, Oksanen et al. 1981, Carpenter et al. 1985) that is, arguably, one of the foundations of modern thinking in community ecology. An important outcome of this body of theory is the prediction that adding carnivores to the basic 2-level consumer–resource chain will have the net result that equilibrium resource abundance will be higher in the three-level chain than in the two-level chain. We now show explicitly that this outcome can derive from two different mechanisms at two different organizational scales.

We present a simple Lotka–Volterra model of three species food chain (Fig. 1A). Using this model we contrast well known trophic cascade results (Oksanen et al. 1981) with those obtained when intermediate species respond to densities of predators and resources. At this point we stress that in this article we do not derive trait responses from some optimality models (e.g. optimal foraging theory; Stephens and Krebs 1986, Houston and McNamara 1999) but we take functional dependencies of these trait changes from empirical studies in order to illustrate some issues relevant to empirical approaches. In this context we also indicate differences in trait and predation mediated effects when propagated up versus down trophic levels.

We begin with the classical model describing tri-trophic interactions among a predator (P), consumer (C), and resource (R) organized in a linear chain (Fig. 1A). As with the original formulations (Rosenzweig 1973, Oksanen et al. 1981) we describe food web dynamics using a Lotka–Volterra predator–prey system extended to three species where

$$\begin{aligned}\frac{dR}{dt} &= rR\left(1-\tfrac{R}{K}\right)-\Lambda_C RC\\ \frac{dC}{dt} &= C(e_C\Lambda_C R - m_C - \Lambda_P P)\\ \frac{dP}{dt} &= P(e_P\Lambda_P C - m_P)\end{aligned} \tag{1}$$

This model assumes that resources grow logistically in the absence of consumers. Parameters Λ_C and Λ_P are cropping rates of consumers and predators, respectively, and e_C and e_P are coefficients representing the efficiency by which prey items are converted into consumer or predator individuals. Also, consumer and predator functional responses ($\Lambda_C R$ and $\Lambda_P C$) are assumed to be linear. In this model, species in higher trophic levels directly affect species in adjacent, lower trophic levels via predator–prey interactions that result in density reductions of prey. Such a model does not explicitly consider the behavioral responses of prey to the presence of predators.

The equilibrium for predation-mediated case (denoted by the sub-index D) is:

$$\begin{aligned}R_D &= K\left(1-\frac{\Lambda_C m_P}{e_P r\Lambda_P}\right)\\ C_D &= \frac{m_P}{e_P\Lambda_P}\\ P_D &= \frac{e_C\Lambda_C}{\Lambda_P}K\left(1-\frac{\Lambda_C m_P}{e_P r\Lambda_P}\right)-\frac{m_C}{\Lambda_P}\end{aligned}$$

There are two conditions that must be satisfied for this system to have a three species equilibrium:

$$e_P > \frac{\Lambda_C m_P}{r\Lambda_P} \text{ and } K\left(1-\frac{\Lambda_C m_P}{re_P\Lambda_P}\right) > \frac{m_C}{e_C\Lambda_C}$$

The first condition implies that there are threshold levels of energy transfer that must be met for a three species system to persist. The second condition compares equilibrial resource density in a food chain with predators (three level chain) and without predators (two level chain). This condition states that the equilibrial resource abundance in a three level chain will be greater than the equilibrial resource abundance in a two level chain whenever predators exist in the food chain. This condition therefore specifies that adding predators will enhance equilibrial resource abundance by way of reducing the equilibrial density of consumers eating the resources. From the formulas for equilibrial species densities we get that

$$\begin{aligned}R_D &= \frac{m_C + \Lambda_P P_D}{e_C\Lambda_C}\\ C_D &= \frac{r(e_C K\Lambda_C - m_C - \Lambda_P P_D)}{e_C K\Lambda_C^2}\end{aligned} \tag{2}$$

which clearly describes the cascading effect: an increase in the equilibrium predator density (P_D) is followed by the decrease in consumer equilibrial density (C_D) which, in turn, leads to increase in the equilibrium resource density (R_D) when compared with the control case where predators are absent. Such a positive indirect effect of predators on resources, mediated by changes in consumer density, is known as a predation-mediated cascading effect (Abrams et al. 1996).

Because the resource abundance is set by the level of nutrients supplied to the resource and K is a surrogate for that level of the nutrient supply (or resource productivity) then the second condition also implies that there will be threshold levels of productivity before consumers and predators can exist as a part of the food chain. The equilibrium conditions then give rise to the familiar step-wise increase in the abundance of trophic levels across a resource productivity gradient (Fig. 2A, upper panel; Mittelbach et al. 1988, Leibold 1989, Schmitz 1992). The lower panel in Fig. 2A shows the interaction strength (measured as the cropping rate)

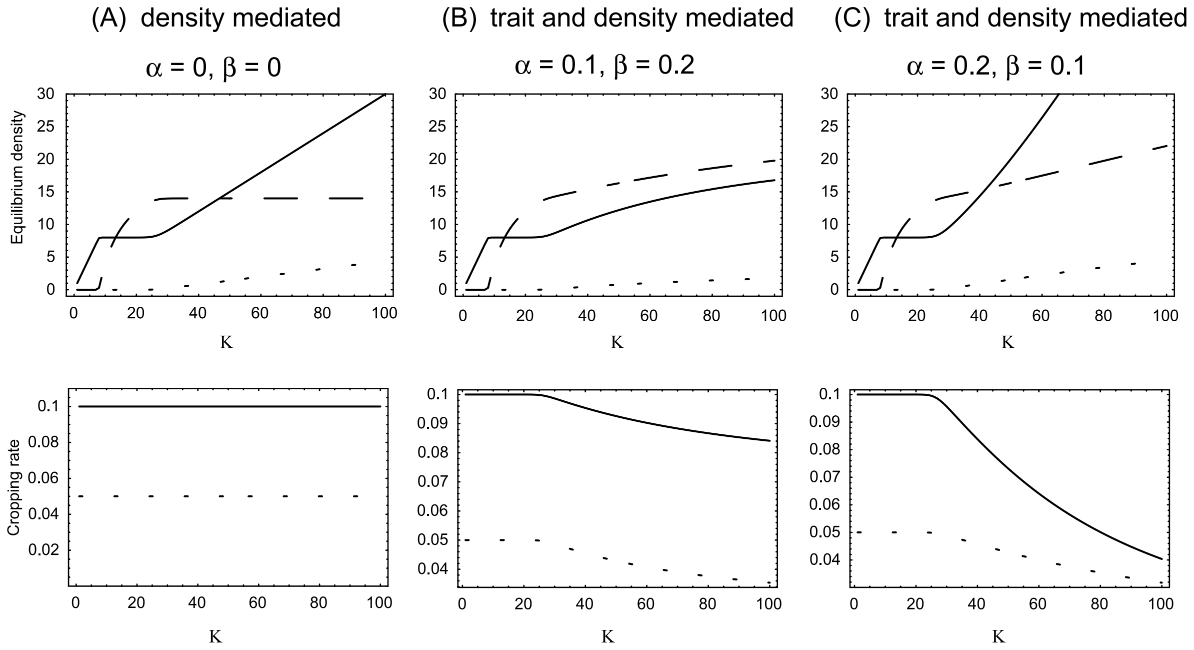

Fig. 2. Density only and combined trait and density mediated interactions in food chains. Top panel shows dependence of the equilibrial resource (solid line), consumer (dashed line) and predators (dotted line) density on the resource carrying capacity K. The bottom panel shows the consumer (solid line) and predator (dotted line) cropping rates at the population equilibrium. Density mediated case assumes that cropping rates are independent of predator densities ($\alpha = \beta = 0$ in Eq. 3 and 4) whilst trait and density mediated cases ($\alpha = 0.1$, $\beta = 0.2$ in the middle panel and $\alpha = 0.2$, $\beta = 0.1$ in the right panel) assume both density mediated interactions and trait mediated interactions modeled as decreased consumers and predators activity with predation risk. Other parameters: $r = 2$, $\lambda_C = 0.1$, $\lambda_P = 0.05$, $m_C = 0.08$, $m_P = 0.07$, $e_C = 0.1$, $e_P = 0.1$.

at the equilibrium which is constant and equal to Λ_C and Λ_P.

In a series of papers, Abrams introduced and elaborated (reviewed by Abrams et al. 1996) the idea that behavioral (trait) responses of consumers to predators can result in a wider range of indirect effects in food webs than those manifested simply via predation effects. The exact outcome depends on the way consumers trade off fitness gain from foraging against the fitness cost due to predation (predation risk) associated with foraging. The insight emerging from Abrams' work is that in order to build behavioral dependencies related to predation risk into a fully dynamic model we must consider the response of consumers to predator density. It is well known in behavioral ecology that consumers respond to predator presence by reducing their foraging activity to minimize predation risk (Sih 1980, 1986, 1987, Mangel and Clark 1986, Lima and Dill 1990, Werner 1992, Houston et al. 1993, Lima and Bednekoff 1999). Decreasing foraging activity is often manifested as a reduction in per capita intake rates of resources by consumers due to decreased consumer activity which we assume is directly proportional to the consumer cropping rate Λ_C (reviewed by Werner and Anholt 1993). The work of Peacor and Werner (2001) suggests that a reasonable approximation for this response is an exponential decrease in consumer search rate (Λ_C) with increasing predator density

$$\Lambda_C(P) = \lambda_C e^{-\alpha P} \tag{3}$$

where α is a proportionality parameter.

The decreased consumer activity necessarily influences the predator cropping rate (Λ_P). Thus, we need to relate the predator cropping rate to consumer and predator activity levels. Several possible functional forms for such dependency were derived in literature (Yapp 1955, Skellam 1958, Werner and Anholt 1993). Here we assume that the predator cropping rate decreases with increased predator level in the same way as consumer cropping rate, i.e.

$$\Lambda_P(P) = \lambda_P e^{-\beta P} \tag{4}$$

where λ_P and β are positive parameters. The logic behind this is that as consumer activity decreases due to increased predation, there will be proportionally less encounters between predators and consumers and, consequently, the predator cropping rate decreases proportionally to the consumer cropping rate.

The equilibrium solutions when substituting $\Lambda_C(P)$ and $\Lambda_P(P)$ in system (1) can be obtained numerically. Comparison of the predation-mediated case only with the combined trait- and predation-mediated case is done in Fig. 2. Figure 2B shows the case where consumer cropping rate decreases more slowly with increased predator density than the predator cropping rate (i.e. $\alpha < \beta$) while Fig. 2C shows the opposite case (i.e. $\alpha > \beta$). These simulations show that a change in the trait either magnify or reduce the cascading effect because the equilibrial resource density for the combined trait- and predation-mediated case will be either higher or lower than is the equilibrial resource density for the predation-mediated case only (Fig. 2A vs 2B, C). This is because the reduction in the consumer cropping rate due to increased predation can be smaller than reduction in the predator cropping rate (Fig. 2B, $\alpha < \beta$) or larger (Fig. 2C, $\alpha > \beta$). Moreover, in the density mediated case the increase in resource level is balanced by the increase in predator density which renders consumer equilibrial density independent of enrichment level. Non-linearities introduced by changes in consumer activity level destroy this perfect balancing and lead to changes in the consumer equilibrium density with the enrichment. Moreover, we observe that both resources and consumers can increase simultaneously in the combined trait and density mediated case while the classical density mediated food chain biomass accrual among organisms at adjacent trophic levels is predicted to be uncorrelated (Fig. 2A; Oksanen et al. 1981, Leibold et al. 1997).

Thus, our results suggest that for food chains which are predominantly bottom-up regulated (i.e. for low environmental productivities measured by the resource carrying capacity (K) the combined density- and trait-mediated effects either promote or reduce trophic cascades because the equilibrium resource levels either increase or decrease when compared with density-mediated food chains. One crucial point emerging from this analysis is that combined trait and density effects produce similar qualitative outcomes at the resource level across the productivity gradient. This indicates that field experiments aimed at testing top-down and bottom-up effects on food chain dynamics must be designed to isolate the effects of behavior from the effects of density. If this is not done, one could arrive at the mistaken impression that density-mediated effects are the important driver of food chain dynamics when in reality trait-mediated effects could be the factor governing dynamics (Schmitz et al. 1997, Schmitz 1998, Peacor and Werner 2000, 2001).

To separate the effects of behavior from the density effects we now make the assumption that predators do not undergo population dynamics but rather influence parameters and variables of the resource–consumer system to which they are linked. For example, we assume that increased predation risk, which arises from increased density of predators, influences community dynamics by changing the values of parameters describing the foraging activity of consumers, i.e. there is plasticity in the parameters describing individual-scale processes. In essence, we are now treating predators as a component of the environment of the consumer–resource interaction (Schmitz 1993, McCauley et al. 1988) in each of the model systems. This also corresponds to most field research programs that explore effects of predators on community dynamics because they simply manipulate the abundance of predators and then examine interactions and dynamics of species lower down in the food web.

Risk predators

We explore this case in two ways. First, we assume that consumers are inflexible (by which we mean they do not respond behaviorally to the presence of predators). So, indirect effects of predators on resources are transmitted by changes in consumer density only. In the second case we assume that consumers are flexible, by which we mean they respond to presence of predators by reducing their activity but predators do not feed on consumers. In this case predators are called risk predators. Now indirect effects are only trait-mediated.

Eliminating the equation describing predator dynamics from the three species model (1) and treating predator density P as a constant leads to the following resource–consumer equilibrium for the density-mediated case (D):

$$R_D = \frac{m_C + \Lambda_P P}{e_C \Lambda_C}$$

and

$$C_D = \frac{r(e_C K \Lambda_C - m_C - \Lambda_P P)}{e_C K \Lambda_C^2}$$

We remark that these equations relating equilibrial species densities are exactly the same as in the case where predators are allowed to undergo dynamics (Eq. 2). The above equilibrium implies that increasing predator density has a positive effect on resources and a negative effect on consumers giving rise again to a trophic cascade when predator density is increased (Fig. 3A, top panel). Similar to the tri-trophic case, resource–consumer coexistence is possible only for environments with high enough productivities ($K > (m_C + \Lambda_P P)/(e_C \Lambda_C)$). In such environments the consumer equilibrial density increases with increasing environmental productivity (Fig. 3A, middle panel). Thus, even when field experiments are constrained by constant predator density, they still should provide a reliable, qualitative test of theory on density-mediated cascading effects.

The interior equilibrium for the combined density- and trait-mediated case (T) is

$$R_T = \frac{e^{P\alpha}(m_C + P\lambda_P e^{-P\beta})}{e_C \lambda_C}$$

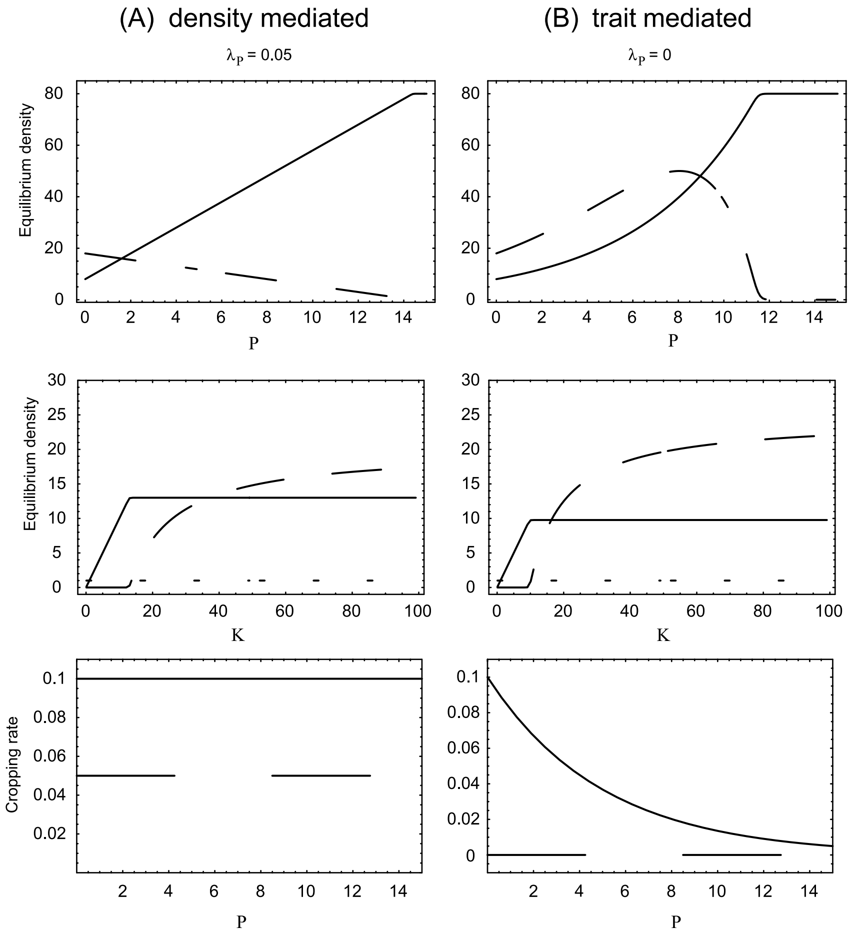

Fig. 3. Density only (left panel, $\lambda_P = 0.05$, $\alpha = \beta = 0$) and trait only (right panel, $\lambda_P = 0$, $\alpha = 0.2$, $\beta = 0.1$) mediated interactions in food chains where predator density is constant. Top panel shows dependence of the equilibrial resource (solid line) and consumer (dashed line) density on predator density P ($K = 80$). Similarly, the middle panel shows dependence of species equilibrium densities on resource productivity K ($P = 1$ in the middle panel). The bottom panel shows the consumer (solid line) and predator (dashed line) cropping rates at the population equilibrium. Other parameters: $r = 2$, $\lambda_C = 0.1$, $m_C = 0.08$, $e_C = 0.1$.

and

$$C_T = \frac{e^{P\alpha} r[e_C K \lambda_C - e^{P\alpha} r(m_C + P\lambda_P e^{-P\beta})]}{e_C K \lambda_C^2}$$

To examine the trait-mediated case (T), we set $\lambda_P = 0$ which means there is no direct predation on consumers. Comparison of the two sets of equilibria (R_D, C_D, Fig. 3A vs R_T, C_T, Fig. 3B) reveals that the net effect of top predators on the food chain is dependent on the nature of the effect of predators on consumers. When predators reduce consumer density, the indirect effect of predators on resources and consumers is linear. When predators cause changes in consumer foraging behavior, the effect of predators on resources and consumers is non-linear because it is manifest in the per capita consumption rate of the consumer $\Lambda_C(P)$ (Fig. 3B, bottom panel). The dependency of the consumer equilibrium on predator density for trait-mediated case is a hump-shaped curve (dashed line in Fig. 3B). As $\Lambda_C(P)$ decreases with increasing P the density of consumers increases because resource density increases due to reduced search rate of primary consumers. If $P > P_{max}$ then the primary consumer equilibrial density decreases with increasing predation risk because increased resource density does not compensate for decreased primary consumer growth rate caused by low consumer activity level. Therefore, in the absence of direct predation, introduction of predation risk can either increase the equilibrial consumer density if decrease in consumer search rate is small, or it can decrease consumer density if the decrease in consumer search rate is large. On contrary to the classical theory of trophic cascades (Fig. 3A) we observe that both resources and consumers can increase simultaneously with increased predator density ($P < P_{max}$). For both density-mediated interactions and trait-mediated interactions we observe a trophic cascade at the resource level. As the dependence of equilibrial resource and consumer density on predator density is highly nonlinear in the trait-mediated case the strength of trophic cascades for the two cases varies with predator density. Thus, for low predator densities we observe that resource increase rate is slightly higher when cascading effect is transmitted by consumer density changes when compared with trait-mediated case. On the contrary, for higher predator densities resource increase rate is higher when cascading effect is transmitted by trait-mediated changes.

In summary, the analysis of top-down and bottom-up manipulations on food chain dynamics illustrate the contrasting ways that density- and trait-mediated effects of consumers influence resource and predator abundance. In the case of top-down manipulations, changes in predator density have a positive indirect effect on resource abundance irrespective of the way top-down effects are transmitted through the consumer trophic level (Fig. 3). This symmetry is not retained for consumers. Consumer density decreases along the predation gradient linearly for density-mediated interactions (Fig. 3A) while if interactions are transmitted by changes in consumer foraging behavior, this dependency is a hump-shaped function (Fig. 3B). Density- and trait-mediated effects along the environmental productivity gradient provide a similar functional dependencies.

The conceptualization that food webs are arrayed in linear chains is a useful framework to start exploring how density-mediated and trait-mediated effects influence food web dynamics. In many instances, however, consumers have the opportunity to choose among resources or habitats that differ in their nutritional value and risk of predation (Peacor and Werner 2000). Such choice involves a trade-off in which consumers may forego the use of resources that provide the greatest nutrient intake rates but at the same time make them highly vulnerable to predation in favor of less nutritious resources that have lesser predation risk (Peacor and Werner 2000). Modeling such trade-offs requires that resources can no longer be treated collectively as a single functional unit. Instead, they must be treated as explicit populations. Consequently, we now must consider more branching food web structure (Fig. 1B).

Apparent competition in two resource food webs

We consider a system in which consumers have a choice among two distinct resources that differ in their net nutritional value (Fig. 1B). These differences arise as a consequence of different gross nutritional content and predation risk leading to a trade-off in net benefit of one vs the other (Peacor and Werner 2000). These resources could be two food types within a habitat or two distinct habitat types on a landscape (Peacor and Werner 2000). The densities of those two resources are denoted as R_1 and R_2. In the interest of applying this theory to field experimentation, we continue with the assumptions that predator density is held at constant treatment levels and the remaining populations are free to vary in abundance.

We begin by extending the model used to describe top down effects on food chains to the two-resource setting. In this model, predator density (P) is fixed and the densities of consumers (C) and resources (R_i) undergo dynamics according to the equations:

$$\begin{aligned}\frac{dR_1}{dt} &= r_1 R_1\left(1 - \tfrac{R_1}{K_1}\right) - \Lambda_{C_1} R_1 u_1 C\\ \frac{dR_2}{dt} &= r_2 R_2\left(1 - \tfrac{R_2}{K_2}\right) - \Lambda_{C_2} R_2 u_2 C\\ \frac{dC}{dt} &= u_1 C(e_1 \Lambda_{C_1} R_1 - m_1 - \Lambda_{P_1} P)\\ &\quad + u_2 C(e_2 \Lambda_{C_2} R_2 - m_2 - \Lambda_{P_2} P) \qquad (5)\end{aligned}$$

We represent consumer preference for a resource (denoted by u_i) simply as the proportion of time spent utilizing that resource. Thus, we have $u_1 + u_2 = 1$. We begin by assuming that consumers prefer resource 1 to resource 2 and that resource 2 serves as a partial or complete refuge from predation. This is modeled by assigning a lower value to predator cropping rates of consumers on resource 2 than on resource 1 ($\Lambda_{P_2} < \Lambda_{P_1}$). When resource 2 is a complete refuge then we set the consumer cropping rate on this resource zero ($\Lambda_{P_2} = 0$). We explore the consequence of shifting preferences due to predation risk on food web dynamics. Thus, if there are no predators, all consumers are assumed to utilize resource 1 ($u_1 = 1$, $u_2 = 0$) and the food web topology is described as a linear food chain. With the addition of predators, consumers forego the use of the more nutritious resource 1 in favor of the less risky resource 2. This means that consumer preference for the second resource (u_2) will be an increasing function of predator density P. These assumptions give rise to the following equilibrium resource and consumer densities:

$$R_{1_D} = \frac{K_1(e_2 K_2 \Lambda_{C_2} u_2(-\Lambda_{C_1} r_2 u_1 + \Lambda_{C_2} r_1 u_2) + \Lambda_{C_1} r_2 u_1(m_2 u_2 + m_1 u_1 + (\Lambda_{P_2} u_2 + \Lambda_{P_1} u_1)P))}{e_1 K_1 \Lambda_{C_1}^2 r_2 u_1^2 + e_2 K_2 \Lambda_{C_2}^2 r_1 u_2^2}$$

$$R_{2_D} = \frac{K_2(e_1 K_1 \Lambda_{C_1} u_1(\Lambda_{C_1} r_2 u_1 - \Lambda_{C_2} r_1 u_2) + \Lambda_{C_2} r_1 u_2(m_1 u_1 + m_2 u_2 + (\Lambda_{P_1} u_1 + \Lambda_{P_2} u_2)P))}{e_1 K_1 \Lambda_{C_1}^2 r_2 u_1^2 + e_2 K_2 \Lambda_{C_2}^2 r_1 u_2^2}$$

$$C_D = \frac{r_1 r_2(e_1 K_1 \Lambda_{C_1} u_1 + e_2 K_2 \Lambda_{C_2} u_2 - m_1 u_1 - m_2 u_2 - (\Lambda_{P_1} u_1 + \Lambda_{P_2} u_2)P)}{e_1 K_1 \Lambda_{C_1}^2 r_2 u_1^2 + e_2 K_2 \Lambda_{C_2}^2 r_1 u_2^2}$$

These equilibria can be used to examine the effects of direct predation, predation risk and both in combination on food web dynamics. If equilibrium consumer and resource population densities are dependent only on the effects of predators on consumer density (density-mediated case), we obtain from the above mathematical expressions linear negative effects of predators on consumer density and linear positive effects on the density of both resources (Fig. 4A, top panel). At low predator densities the consumer equilibrial density will be high and apparent competition between the two resources which is mediated by common consumers can lead to exploitative extinction of the competitively weaker resource (resource 2, lower solid line in Fig. 4A). Consequently, the resulting food web topology will be of the linear food chain. As predator density increases, consumer equilibrial density decreases which weakens the strength of apparent competition and both resources can coexist. Thus, predators indirectly cause both resources to coexist, due to decreasing consumer equilibrial density (dashed line in Fig. 4A). This is another example of density-mediated indirect interactions in food webs with two resources. It follows that along the predator gradient we observe a shift in the food web topology from a linear food chain to a food web with two resources (Fig. 5A).

Now we consider behaviorally mediated effects of predators on the food web. We assume that consumer preference for the first patch (the preferred patch) exponentially decreases with increased predator densities in that patch, i.e.

$$u_1(P) = e^{-\gamma P} \tag{6}$$

where parameter γ is the strength with which consumers react to the presence of predators. High values of this parameter mean that consumers react to low predator numbers, while low values mean that consumers are insensitive to predators. First we assume the trait-mediated case only where risk predators do not feed on consumers but they cause consumers to move to the refuge (patch 2). This is modeled by setting the predators cropping rates in both patches equal to zero ($\lambda_{P_1} = \lambda_{P_2} = 0$) in model (5). Figure 4B (top panel) shows the change of species equilibrial densities along the predator density gradient. Without predators, consumers are in the more preferred patch 1 and there is no apparent competition between the two resources. As predator density increases, consumers start to move to refuge (patch 2, Fig. 4B, middle panel where solid line is the preference of consumers for patch 1 and dashed line for patch 2), which causes apparent competition between the two resources. Because consumer equilibrial density initially increases as a consequence of using the alternative patch where consumers are protected from predation, resource 1 density first decreases, because the apparent competition outweighs the decrease in consumption of resource 1 by consumers. For yet higher predator densities, resource 2 is outcompeted by resource 1. As consumer preference for the alternative habitat increases further on, effects of apparent competition vanish because consumer density decreases and the system tends to the resource 2–consumer–predator food chain because consumers tend to move to patch 2. Resource 1, being practically excluded from consumer diet, tends to its carrying capacity (which equals to 50 units in Fig. 4). We remark that the apparent competition between resources was mediated here by consumer behavior. Thus, this is an example of indirect interactions between resources which are caused by trait-mediated apparent competition. The corresponding changes in food web topology along predator density gradient are shown in Fig. 5B. For low predator densities the corresponding food web topology at species equilibrium is described by a food web with two resources where consumers preference is biased to resource 1. As predator density increases, the food web topology can become a linear food chain as the less profitable resource is outcompeted through apparent competition. For yet higher predator densities the food web topology is again of two-resource–consumer–predator food web, but consumers preference is biased toward resource 2.

Figure 4C shows combined density- and trait-effects on species equilibrium densities. In this figure we assume that predators feed on consumers which, in turn, switch their habitat preferences. We observe that due to direct predation, the equilibrium consumer density is lower than in the trait-mediated case only. This weakens the apparent competition between resources and leads to coexistence of both resources along the predator gradient.

Figure 4D shows combined effects of habitat shift and decrease in consumer activity level as a response to increased predation risk on species equilibrium densities. This figure assumes that predators do not feed on consumers (no density effects; $\lambda_{P_1} = \lambda_{P_2} = 0$) and that decrease in consumer activity level (shown in bottom panel) in patch 1 (solid line) is more rapid than in patch 2 (which is a partial refuge; dashed line). This pattern is very similar to the case of habitat shift only, except that decrease in consumer activity level weakens slightly apparent competition between resources due to lower consumer equilibrial densities.

Figure 4E shows combined density and trait (habitat shift and decrease in consumer activity level) on species equilibrium densities. Again, the resulting pattern is similar to that of trait (habitat shift only) and density mediated case.

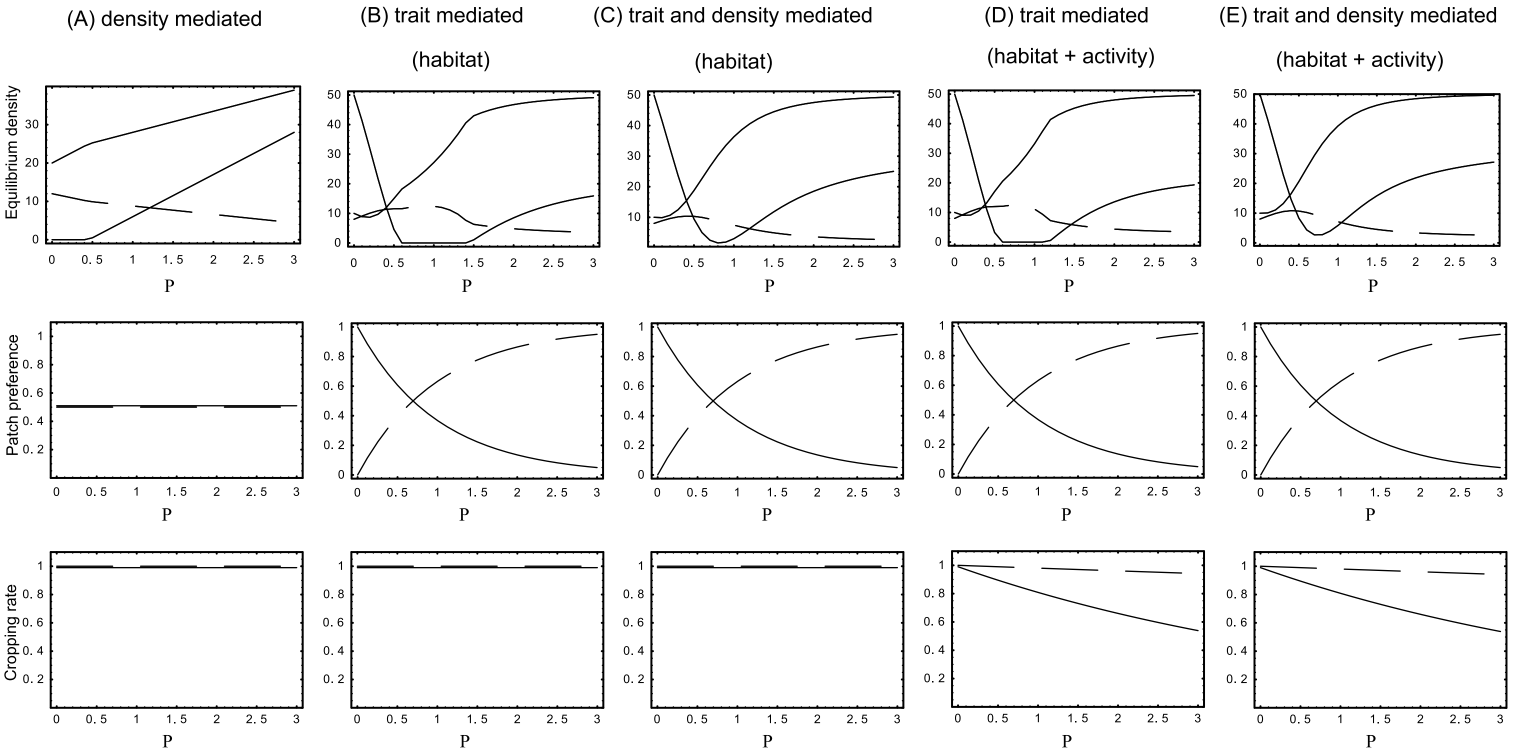

Fig. 4. Density only and combined trait (habitat shift and/or decrease in consumer activity level) and density mediated interactions in food webs with two resources. Top panel shows dependence of the equilibrial resource density in patch 1 (solid line), in patch 2 (solid line) and consumer density (dashed line) on predator densities. The middle panel shows corresponding habitat preferences of consumers (solid line shows preference for better patch 1, while the dashed line shows preference for the alternative patch 2). The bottom panel shows the consumer activity level when feeding on resource 1 (solid line) and on resource 2 (dashed line). In the density-mediated case consumer preference for either patch is independent from predator density ($u_1 = 0.5$, $u_2 = 0.5$, $\alpha_1 = \alpha_2 = \beta_1 = \beta_2 = 0$, $\lambda_{P_1} = 0.1$, $\lambda_{P_2} = 0.02$). The trait-mediated case (habitat shift) assumes that predators cannot feed on consumers but they undergo habitat shift with increased predator densities ($\lambda_{P_1} = \lambda_{P_2} = 0$, $\gamma = 1$, $\alpha_1 = \alpha_2 = \beta_1 = \beta_2 = 0$). The combined trait and density-mediated case (habitat shift) assumes that predators feed on consumers and consumers undergo habitat shift ($\lambda_{P_1} = 0.1$, $\lambda_{P_2} = 0.02$, $\gamma = 1$, $\alpha_1 = \alpha_2 = \beta_1 = \beta_2 = 0$). The other two cases where consumer activity decreases are combination of the previous cases where, in addition, consumer activity level decreases with increased predator density ($\alpha_1 = \beta_1 = 0.2$, $\alpha_2 = \beta_2 = 0.02$.) Other parameters: $r_1 = 1$, $r_2 = 0.5$, $\lambda_{C_1} = 0.1$, $\lambda_{C_2} = 0.1$, $K_1 = 50$, $K_2 = 50$, $m_1 = m_2 = 0.1$, $e_1 = 0.1$, $e_2 = 0.05$.

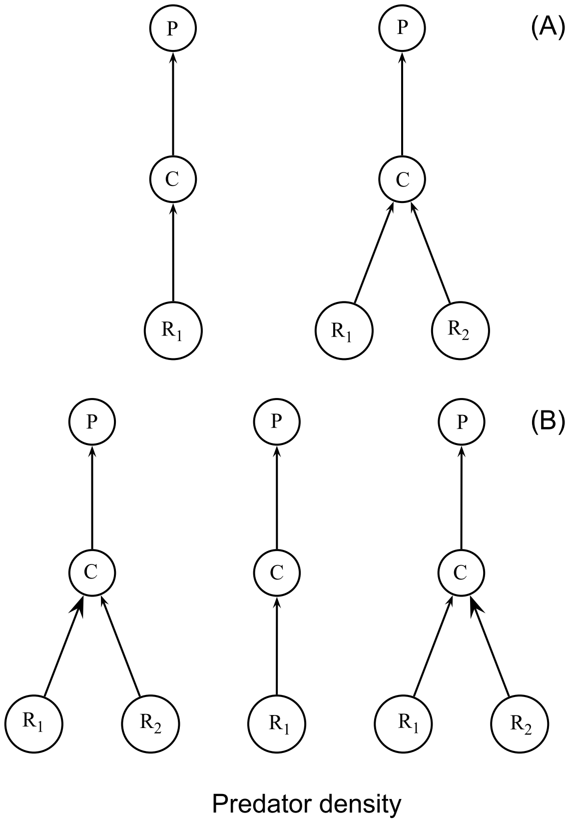

Fig. 5. Switch in food web topologies along predator density gradient. (A) assumes density-mediated interactions, while (B) assumes trait-mediated interactions (risk predators).

Discussion

We explore here how indirect effects in food webs may arise when top predators directly influence the way consumers impact their resources. These indirect effects can emerge via two classes of mechanism. The first, called density-mediated indirect effects, arise when one species (A) indirectly affects another (B) by changing the abundance of intermediate species that interact with both species A and B. This is the kind of effect predicted by classical theory that models dynamics wholly at the population scale. The second, called trait-mediated indirect effects, arise when one species (A) modifies the way two other species (B and C) interact at the individual-scale by causing changes in the behavior, morphology or life-history of the intervening species (B).

We compared indirect effects in simple food webs arising from changes in density of intervening species with those that are transmitted via changes in intervening species' traits. We focused on two traits related to consumer foraging activity – decreased activity and habitat switch under predation risk – that lead to two types of indirect interactions: trophic cascade and apparent competition. We also examined how bottom-up and top-down manipulations alter the nature and strength of these indirect effects.

Theory on bottom-up manipulation of density mediated regulation in food chains predicts that species abundances in all trophic levels will never decrease with increased enrichment level and species abundances in adjacent trophic levels is uncorrelated because along the enrichment gradient one of these two species is always at a constant level (Fig. 2A; Leibold et al. 1997). We have shown here that if the food chain is driven by both trait and density mediated interactions then abundances of all trophic levels will likewise never decrease with increased enrichment level. But, densities of all three species can be correlated so they will increase simultaneously along a productivity gradient (Fig. 2B, C). Theory on top-down regulation of food chains predicts that with increased predator density the consumer density will decrease while the resource density will increase (trophic cascade) when interactions in food chain are strictly density mediated (Fig. 3A). In contrast, our analysis of food chain dynamics in which consumer activity level changes with increased predation risk reveals that both resource and consumer densities can increase simultaneously with increased predator density (Fig. 3B). Such a pattern was observed in certain food webs reviewed in Leibold et al. 1997).

This pattern was also observed when we altered the topology of the food web from a linear chain to food webs with two resources. Whenever interactions are solely density mediated then we observe that both resources never decrease and consumers never increase along the predator density gradient (Fig. 4A). This picture changes qualitatively if trait-mediated interactions are considered alone, or in combination with density-mediated interactions (Fig. 4B–E). In these latter cases, resource density can decrease and consumer density can increase along the predator density gradient (especially at low to medium predator densities) which is inconsistent with the classical theory of trophical cascades. In essence, predation can cause the nature of the cascading effects to be altered depending on the way the interactions are transmitted.

For density mediated interactions we see the system display a community cascade, sensu Polis (1999), in which the indirect effects of top predators are manifested among both resource species that increase (Fig. 4A); when interactions are trait mediated (habitat shift) we see the same system switch to a species cascade, sensu Polis (1999), in which the indirect effects are manifested narrowly in a single resource species which increases when predator density increases (for low predator densities in Fig. 4B–E).

Despite these differences, our results show that in many respects trait-mediated indirect interactions can have similar directional effects as density mediated interactions. Thus, these two types of interactions may be difficult to distinguish in natural and experimental systems because they will mask one another. Experiments should be designed to separate density and trait effects in order to understand what are the main driving forces in structuring food webs. The potential for trait-mediated effects to have an overriding influence on food web dynamics may be high for two reasons. First, there are inherent non-linearities in the relationship between foraging traits of consumers and equilibrium abundances or consumers and resources. Such non-linearities are far less apparent in density-mediated cases. Second, the strength and duration of trait-based effects can be similar to those resulting from density-based interactions. This then begs the question: How many studies in the past have incorrectly attributed predation effects on communities to be the result of density-mediated effects rather than trait-based effects?

Recent studies examining the effects of adaptive behavior on food web dynamics (Abrams 1984, Gleeson and Wilson 1986, Abrams and Matsuda 1993, Křivan 1996, 1997, Fryxell and Lundberg 1997, van Baalen et al. 2001, Křivan and Schmitz 2003) focus on the effects of consumer diet choice on food web dynamics, and as such only examine dynamics that are driven by changes in prey species densities, not prey species behavior. Here we extend those kinds of analyses by incorporating explicit functions, estimated from experimental observations, that integrate consumer foraging and prey behavioral responses to predation risk. Unlike the previous analyses, however, we only assume flexible behavior and so do not postulate that consumers trade off predation risk and their foraging effort in order to maximize fitness. The difficulty in taking a strictly optimization approach of fitness maximization is that solutions hinge explicitly on the choice of fitness function. For example, in the food chain model considered in this article if consumers behave so that their per capita population growth rate maximizes (which is often taken as a proxy of animal fitness) then at the population equilibrium consumers should always feed at the maximum possible rate regardless of predation risk. In contrast, if predation risk increases quadratically as a function of foraging activity and resource consumption rate increases linearly then consumers should forage at some intermediate rate Abrams (1984). We opted for the simpler functionality here because it is supported by empirical evidence (Peacor and Werner 2001) while still conveying the qualitative essence of the point that trait effects can lead to different dynamics than density effects.

The problem in identifying their relative importance is that trait-based effects (especially due to behavior) often remain "masked" by density effects. "Unmasking" the amount of variation in consumer and resource abundance that is attributable to trait effects requires that we conduct field experiments on communities in different ways than would be prescribed by classical theory. Specifically, field experiments cannot simply manipulate predator density. They must also be designed to "switch on and off" the act of direct predation. This is followed by comparisons of the net effects of trait changes alone with the net effects of trait and density changes operating simultaneously. This highlights the point that community ecologists need to change the way experiments are conducted on natural systems in order to unravel the relative importance of different causal mechanisms driving community-level interactions.

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