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Trophic cascades : the primacy of trait-mediated indirect interactions

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REVIEW

Trophic cascades: the primacy of trait-mediated indirect interactions

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Abstract

Trophic cascades are textbook examples of predator indirect effects on ecological systems. Yet there is considerable debate about their nature, strength and overall importance. This debate stems in part from continued uncertainty about the ultimate mechanisms driving cascading effects. We present a synthesis of empirical evidence in support of one possible ultimate mechanism: the foraging-predation risk trade-offs undertaken by intermediary species. We show that simple trade-off behaviour can lead to both positive and negative indirect effects of predators on plant resources and hence can explain considerable contingency on the nature and strength of cascading effects among systems. Thus, predicting the sign and strength of indirect effect simply requires knowledge of habitat and resource use by prey with regard to predators' presence, habitat use and hunting mode. The synthesis allows us to postulate a hypothesis for new conceptualization of trophic cascades which is to be viewed as an ultimate trade-off between intervening species. In this context, different predators apply different rules of engagement based on their hunting mode and habitat use. These different rules then determine whether behavioural effects persist or attenuate at the level of the food chain.

Keywords

Adaptive foraging, anti-predator behaviour, cascading effects, density-mediated indirect effects, food chains, food web topology, predation risk-foraging trade-offs, predator identity, predator–prey interactions, trait-mediated indirect effects.

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INTRODUCTION

The idea that ecological communities can be viewed as linear chains of interacting carnivores, herbivores and plants is arguably one of the most powerful conceptualizations of modern community ecology (Fretwell 1987). This view led to the prediction of an important phenomenon known as trophic cascade (Paine 1980; Carpenter *et al.* 1985). Trophic cascades – the indirect effects of carnivores on plants mediated by herbivores – occur in a wide variety of systems (Shurin *et al.* 2002). Their discovery has been hailed as one of the most exciting successes in food web ecology (Strong 1992; Polis *et al.* 2000), and make excellent textbook examples of indirect effects in communities (Polis *et al.* 2000). Over the last 10 years, there has been lively debate about their nature, strength and overall importance (Strong 1992; Polis & Strong 1996; Pace *et al.* 1999; Persson 1999; Polis 1999; Polis *et al.* 2000; Shurin *et al.* 2002). Even so, there is continued uncertainty about the ultimate mechanism(s) causing variation in the nature and strength of trophic cascades.

We present a synthesis of empirical evidence to support one possible ultimate mechanism driving trophic cascades, namely prey antipredator behaviour. Emerging empirical support suggests that antipredator behaviour acts in addition to, or in place of, classic numerical effects of predators on prey to determine the sign and strength of indirect effects on plants. We present here a review of that empirical evidence and postulate a hypothesis for new conceptualization of trophic cascades.

Background

Theory on food chain interactions has developed from two different perspectives: population ecology and evolutionary ecology. The two perspectives agree on the factor that causes cascading effects (i.e. carnivores preying on herbivores), but disagree about mechanistic nature of the carnivore effect. The classic population ecological perspective (e.g. Hairston *et al.* 1960; Rosenzweig 1973; Oksanen *et al.* 1981) is that carnivores cause numerical reductions in herbivore

populations by directly killing them. As fewer herbivores translate into lower impacts on plants, carnivores have a positive (beneficial) indirect effect on plants. As the indirect effect is mediated by changes in herbivore population density, it is called a density-mediated indirect interaction (DMII) (Abrams 1995; Werner & Peacor 2003).

Classical theory assumes that herbivores (and all prey for that matter) simply submit passively to their fate. Yet, evolutionarily it makes little sense for prey to simply allow themselves to be captured by their predators. Instead, prey should adopt adaptive foraging strategies that reduce or eliminate predation risk (Mangel & Clark 1988; Lima & Dill 1990; Abrams 1995; Lima 1998, Lima 2002; Sih *et al.* 1998, 2000). Consequently, the mere presence of predators in a community can force prey to make behavioural choices between vital activities such as feeding and avoiding contact with predators. Avoiding carnivores detracts from foraging, which also causes reductions in herbivore impacts on plants (Abrams 1984, 1992, 1995). But now, the indirect effect of carnivores on plants derives from evasive behaviour of herbivores (an individual trait). This kind of indirect effect belongs to a broader class known as behavioural or trait-mediated indirect interactions (TMII) (Kerfoot & Sih 1987; Abrams 1995; Werner & Peacor 2003).

There is a challenge to resolve the importance of trait-mediated trophic cascades because carnivore direct effects on local herbivore density may arise through different potentially simultaneous mechanisms. Carnivores can reduce herbivore density by hunting and killing them, by causing them to disperse and seek refuge, or both. Thus, any behavioural effect of predators on prey will remain 'masked' whenever we measure the net effects of predators simply as local density responses of prey. Unmasking trait effects requires experimentally preventing or 'switching-off' direct predation to reveal only risk effects.

Risk effects can be evaluated using field observations of predator harassment or using experiments that induce only predation risk by either chemical cues (e.g. Peckarsky & McIntosh 1998; Turner *et al.* 2001), predator mouthpart alteration to prevent killing prey (e.g. Wissinger & McGrady 1993, Schmitz *et al.* 1997) or caging predators within larger experimental arenas (e.g., Peacor & Werner 2001). Such methods have revealed trait-mediated cascading effects in a variety of systems.

UNMASKING TRAIT EFFECTS

Cascading effects among carnivores, herbivores and plants in three- and four-level systems

We identified 10 studies that used one or more of the above methods to evaluate risk effects on interactions among plants, herbivores and carnivores (Table 1). The cases cover the same broad range of ecosystems examined in an earlier synthesis of trophic cascades (Shurin *et al.* 2002), namely streams and rivers (Power *et al.* 1985; McIntosh & Townsend 1996; Peckarsky & McIntosh 1998), ponds (Turner 1997; Gelwick 2000; Bernot & Turner 2001), lakes (Carpenter *et al.* 1987), rocky intertidal seahores (Trussell *et al.* 2002), terrestrial old fields (Messina 1981; Beckerman *et al.* 1997), cotton fields (Rudgers *et al.* 2003) and tropical forests (Gastreich 1999). The studies include various vertebrate and invertebrate consumer taxa (Table 1) and a host of plant taxa (Table 1). These studies offer unequivocal evidence that trait-mediated interactions can determine the sign and strength of indirect effects of predators on plants.

It is particularly noteworthy that in revisiting some classic examples of cascading effects customarily thought to arise from DMII, we found that they too may be driven ultimately by TMIIs. Lubchenco (1978) showed that green crabs (*Carcinus maenas*) have a strong positive indirect effect on fucoid algal species diversity and abundance by virtue of a consumptive predator–prey interaction between green crabs and herbivorous *Littorina* snails. However, Trussell *et al.* (2002) offer a different interpretation. They experimentally prevented predation by placing crabs in small perforated tubs within plots containing *Littorina* and fucoid algae. Crabs were fed *Littorina* to elicit predation cues. Cues emanating from the tub caused free-living snails to reduce their feeding in nearby algal patches. The net community level effect was qualitatively similar to that observed in Lubchenco's study indicating that trait effects may have been the ultimate driver of the community level effect. Carpenter *et al.* (1987) conducted experiments with a four-level food chain in which bass preyed on minnows, minnows preyed on zooplankton and zooplankton preyed on phytoplankton. The expectation for this system, based on the hypothesis of DMII, was that bass removal/minnow addition should decrease zooplankton biomass because of heightened predation by minnows with attendant increase in phytoplankton abundance. This outcome did not occur. Instead, there was a reduction in phytoplankton abundance. This effect resulted from strong young-of-year bass recruitment. The heightened predation risk from bass caused minnows to move inshore to shallower waters (a habitat shift) thereby releasing zooplankton from predation pressure – a largely trait-mediated effect (Carpenter *et al.* 1987).

Cascading effects among higher trophic levels

Evolutionarily, any species that is subject to predation risk must respond flexibly to balance fitness gains from foraging

Table 1 Summary of studies demonstrating trait-mediated cascading effects

Study system	Trait effect in middle species*	Sign of indirect effect of top predator on plants	References
	Trophic cascades, three-level systems		
Stream			
Bass–**minnows**–algae	Habitat shift	+	Power *et al.* (1985)
Trout and galaxais–**mayfly**–algae	Reduced feeding because of refuge seeking	+	McIntosh & Townsend (1996)
Trout cue–**mayfly**–algae	Reduced feeding	+	Peckarsky & McIntosh (1998)
Stonefly–**mayfly**–algae	Habitat shift	+	Peckarsky & McIntosh (1998)
Pond			
Predatory cue–**snail**–algae	Reduced feeding	+	Turner (1997)
Bass–**minnows**–algae	Habitat shift	+, −	Gelwick (2000)
Bass–**crayfish**–algae	Reduced feeding	+	Gelwick (2000)
Sunfish–**snails**–periphyton	Habitat shift	+, −	Bernot & Turner (2001)
Crayfish–**snails**–periphyton	Habitat shift	+, −	Bernot & Turner (2001)
Old field			
Ants–**beetles**–*Solidago*	Reduced feeding	+	Messina (1984)
Spiders–**grasshoppers**–plants	Reduced feeding and habitat shift	+, −	Beckerman *et al.* (1997)
Cotton field			
Ants–**caterpillars**–cotton plants	Reduced feeding and spatial shift	+	Rudgers *et al.* (2003)
Intertidal			
Predation cue–**snails**–algae	Reduced feeding	+	Trussell *et al.* (2002)
	Trophic cascades, four-level systems		
Tropical forest			
Spiders–**ants**–beetles–*Piper* plants	Habitat shift	−	Gastreich (1999)
Lake			
Bass–**minnows**–zooplankton–phytoplankton	Habitat shift	−	Carpenter *et al.* (1987)
	Other cascading effects		
Stream			
Fish–**salamanders**–isopods	Reduced feeding because of refuge seeking	+	Huang & Sih (1991)
Pond			
Bass–**Bluegill sunfish**–Zooplankton	Habitat shift	+	Turner & Mittelbach (1990)
Lake			
Pike and lg. Perch–**sm. Perch**–zooplankton	Habitat shift	+	Diehl & Eklov (1995)

*Middle species is highlighted in bold under study system.

against fitness losses from predation risk. In systems where penultimate predators mediate interactions between top predators and herbivores, the penultimate predators should display behaviours similar to herbivores. Indeed, they do (Table 1): top predators have been shown to exert strong indirect effects on herbivore species through trait-mediated interactions with penultimate predators in streams (Huang & Sih 1991), ponds (Turner & Mittelbach 1990) and lakes (Diehl & Eklov 1995).

Synthesis

Experimentally preventing or switching-off predation has revealed important behavioural mechanisms underlying cascading effects (Table 1). Those mechanisms involve disarmingly simple herbivore foraging-predation risk trade-offs that lead to predictable indirect effects of predators on plants. The trade-off can involve reducing foraging activity to increase vigilance, leading to higher plant biomass in the presence of predators than in their absence, as anticipated by earlier theory (Abrams 1984). The sign of this indirect effect is identical to classic density-mediated cascades. The trade-off can also involve a habitat shift where herbivores seek safety in habitats offering poor-quality resources at the expense of high energetic gains in highly risky habitats (Table 1). In these cases, carnivores have a positive indirect effect on high quality, risky resources and a negative indirect effect on refuge resources.

Many studies reviewed here merely demonstrate a trait-mediated cascade. Thus, it remains uncertain whether such TMIIs are generally more important than DMIIs. Furthermore, the intensity of predation and risk were not manipulated, so it remains unclear whether risk and predation effects are generally additive, compensatory (i.e. predators eat that proportion of the population that would have died from intraspecific competition or natural causes if predators were absent), or interactive (Peacor & Werner 2001). Gaining this insight requires conducting new kinds of experiments that disentangle mortality effects from behavioural effects (see Peacor & Werner 2001).

Our synthesis argues for moving away from a classic linear chain conceptualization of food webs. Our reasons for this go beyond those raised in earlier critiques (e.g. Leibold 1996; Polis & Strong 1996) and include the need to consider the topology of the system, the way species are aggregated (community vs. species cascades), the appropriate organizational and temporal scales for predicting indirect effects and the role of predator identity on trophic interactions.

RECONCEPTUALIZING THE ECOLOGICAL SYSTEM

System topology

The idea that species can be assigned to distinct trophic levels implies that all species within a trophic level have similar effects on communities, i.e. they are functionally equivalent entities. Such an aggregation (Fig. 1) leads to the argument that detecting true trophic cascades (community cascades, *sensu* Polis 1999) requires measuring total plant tropic level biomass (Strong 1992). However, in some carnivore–herbivore–plant systems (Table 1), the herbivore trade-off behaviour involved a shift between two functionally distinct groups of resources. In this case, interactions among the basal two trophic levels must be described as a single consumer two-resource system (Fig. 1). In such configurations, resource switching by herbivores can cause strong, compensatory responses in biomass production of the plant categories, whereas total trophic level biomass remains unaltered. Consequently, measuring total plant biomass can give the misleading impression that top predators have weak if any indirect effect on plants (e.g. Strong 1992; Shurin *et al.* 2002). The fact that consumers engage in behavioural trade-offs means that we need to consider a food chain topology that deliberately recognizes flexibility of consumers to switch resources (see also Krivan & Schmitz 2003).

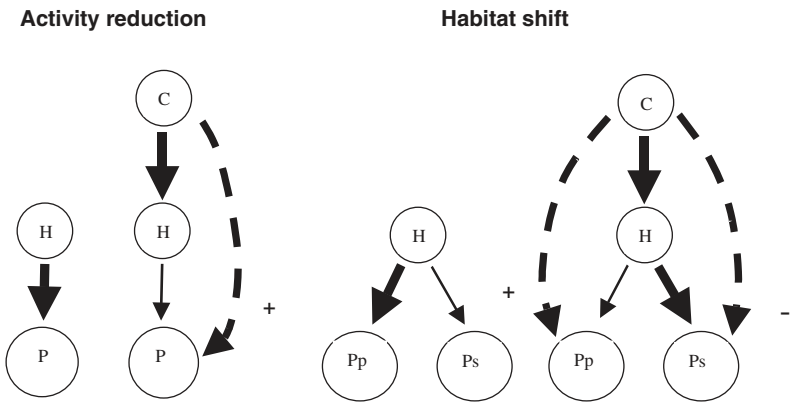

Figure 1 Food web topologies and indirect effects resulting from behavioural avoidance of predators (C) by herbivores (H). Solid lines are direct interactions, dashed lines are indirect interactions. Thickness of arrows indicates interaction strength. The figure shows food web interactions in the absence and presence of predators. Herbivore activity reduction reduces damage to plants (P) and hence leads to a positive indirect effect of predators on plants. Herbivore habitat shift leads to lower damage to preferred plants (Pp) and increased damage to safe plants (Ps). This causes positive and negative indirect effects of predators on plants.

Species aggregations

Community vs. species cascades

Most cascading effects involve a subset of the entire community, so they should more appropriately be called species cascades (*sensu* Polis 1999) rather than true trophic cascades (Polis *et al.* 2000). The implication of such taxonomy is that cascading effects are expected to be comparatively minor interactions in communities because they involve only a few species in an otherwise highly species rich system (Polis *et al.* 2000).

The trait-mediated cascading effects summarized above all accord with a species cascades definition. Nevertheless, prey habitat shifts can precipitate dramatic and lasting changes in the species make-up of the entire plant community with corresponding changes in ecosystem functions such as plant production (Carpenter *et al.* 1987; Schmitz 2003a). Thus, many species within a trophic level may have weak effects and so are not functionally equivalent to a dominant species. Yet species cascades transmitted by behavioural shifts among a few dominant species can have dramatic effects on plant communities. The advantage of using a species cascades perspective is not that it supposes minor interactions in complex systems but rather it focuses attention on the potential for trade-offs among interacting species.

Attenuation of top-down effects

Carnivore effects on plants are thought to be weak in general (Strong 1992). This is because in most species rich systems, species interact directly and indirectly in highly interconnected networks. So, the effects of any one species should diffuse among many interaction pathways causing carnivore effects to attenuate before reaching the plants.

This hypothesis was tested explicitly by evaluating the indirect effects of a spider carnivore on grass and herb biomass in old-field interaction webs through its interactions with generalist and grass-specialist grasshopper species (Schmitz 1998). Interaction pathways between the spider and the plants (i.e. degree of reticulation in food web structure) were manipulated by using different combinations of generalist and specialist grasshopper species. The experiment also manipulated the modality of predator–prey interactions using natural spiders (predation spiders) and spiders with glued mouthparts (risk spiders) to isolate DMIIs from TMIIs. The experiment revealed that indirect spider effects on plants were stronger in the reticulate food webs than in linear food chains (chains comprised of the spider predator, specialist grasshopper and grasses). In the reticulate webs, the generalist grasshopper shifted its habitat use from nutritious grasses to safer but less nutritious herbs in response to predation risk. This habitat shift led to impacts on all plants that swamped out the effects of the specialist herbivore within the same system. This again shows that a conclusion that cascading effects may be weak or non-existent (Strong 1992; Shurin *et al.* 2002) may be an artefact of the way species in a system are aggregated, i.e. the conclusion may be dependent on a particular conceptualization of system topology.

Organizational scale: trait variation and strength of cascades

As a first approximation, it would seem that simply knowing the qualitative nature of the predation risk-foraging trade-off is sufficient biological detail to predict the strength of community interactions. However, populations are ensembles of individuals that vary in phenotypic traits such as age, size and physiological condition. Such trait differences may uniquely determine how individuals trade-off foraging gains against predator avoidance and the likelihood of being captured (Mangel & Clark 1988; Ludwig & Rowe 1990; Abrams & Rowe 1996). Predators that selectively hunt prey with lower physiological condition (old or weak individuals) or smaller size, may weaken prey competitive interactions more so than predators that randomly select prey, leading to altered prey life-cycle development (Agrawal 2001; Werner & Peacor 2003). Thus, the phenotypic state of the prey cohort may have a key effect on trophic interactions (Agrawal 2001; Persson & DeRoos 2003). Therefore, this raises the following key question: to what extent can intraspecific trait variation be safely abstracted while still achieving an accurate generalization of cascading effects in food webs?

One key trait is herbivore body size because it determines the kind and amount of resources individuals can exploit and their vulnerability to predation. Body size-dependent responses to food and predators may be particularly crucial for organisms with non-overlapping generations that live in seasonal environments (Mangel & Clark 1988; Ludwig & Rowe 1990; Abrams & Rowe 1996). Basic allometric rules suggest that herbivore body size should be positively related to damage the herbivore inflicts on plants (Belovsky 1986, 1997). Alternatively, state-dependent models predict that initially smaller individuals that require longer time to mature may have lower fitness than individuals who mature more rapidly because of an initial size disadvantage (Abrams & Rowe 1996). If the cost of avoiding predators in small individuals is a complete failure to mature by the end of the season, then initially smaller individuals may feed more frequently than larger individuals despite the existence of some non-zero level of predation risk (Mangel & Clark 1988; Abrams & Rowe 1996). The question is: how do the opposing effects of allometry and state-dependence interact to determine the nature and strength of the indirect effect of predators on plants?

This question was addressed experimentally in an old-field system using *Pisaurina mira* spiders, *Melanoplus femurrubrum* grasshoppers, and grasses and herbs (Ovadia & Schmitz 2002). Early development stage grasshoppers were sampled to generate a body size frequency distribution. Experimental grasshopper populations were created by sorting individuals into three body size classes based on this distribution: large individuals were those in the uppermost 5% of the frequency distribution; small individuals were those in the lowest 5% of the frequency distribution; and average individuals were those from the middle portion of the frequency distribution. The size treatments were then crossed with two spider predation treatments (spider present and absent) in a fully replicated design and the experiment was run until all grasshoppers developed into adults. Grasshoppers in small size classes suffered higher mortality but exhibited higher growth rates over the course of the season, than grasshoppers in the two larger size classes (Ovadia & Schmitz 2002). Such higher growth rates were sustained by higher foraging effort. The net effect of a lower density of smaller grasshoppers appeared to be compensated by greater per capita foraging effort of the surviving individuals. Consequently, there were no size-dependent differences in net damage level on grasses and herbs in either predator or no predator treatments. Thus, abstracting effects of trait variation and simply representing indirect interactions by their mean effects may be warranted in some cases. Nevertheless, it remains generally unclear whether or not size variation should be used in models of community dynamics because of a shortage of empirical information (Persson & DeRoos 2003).

Temporal scale: fast vs. slow dynamics

The implicit assumption in models of trophic interactions that predict DMIIs is that food web dynamics can be sufficiently characterized by describing interactions wholly at the population scale. It is understood that model parameters governing species population growth rates may be determined by mechanisms below the population scale (e.g. the consumer foraging behaviour). However, it is assumed that such lower-scale processes become invariant over the time scale of population growth because they operate faster (hours to weeks) than do population scale processes (months to years). Thus behaviour effects should equilibrate or attenuate on the time scale of population dynamics.

All the studies in Table 1 were conducted on short time scales (i.e. at most within a single field season), so it remains uncertain whether behavioural responses do indeed matter over the long-term. One recent study, explicitly designed to evaluate the long-term affects of herbivore antipredator responses, indicates that chronic antipredator behaviour does matter (Schmitz 2003a). The study built on short-term insights (Beckerman *et al.* 1997) about the antipredator habitat shift to safer herbs undertaken by the grasshopper herbivore *M. femurrubrumin*. One preferred herb species *Solidago rugosa* is a competitive dominant plant in the old field system. Thus habitat shift by grasshoppers should cause *S. rugosa* abundance to be suppressed and less competitive herbs species to be released – thereby altering plant species evenness. This hypothesis was tested by systematically excluding either predators (two-trophic level food web), or predators and herbivores (plants only) from 2 m × 2 m field plots and measuring the effects on plant species abundance and plant productivity relative to control plots that represented the natural field state. Three years of sustained predator, and predator and herbivore exclusion resulted in lower plant species evenness and higher plant biomass production than control field plots representing the intact natural three-trophic level system. Thus chronic antipredator behaviour of herbivores can have predictable impacts on community structure and function that are indeed manifest on the time scale of population and community dynamics (Lima & Bednekoff 1999; Sih *et al.* 2000).

Predator identity and the nature of indirect effects

Most predator–prey theory assumes that all predator species elicit qualitatively similar risk responses in their prey. Classical theory assumes that predators cause no risk responses. Evolutionary ecology theory alternatively assumes that predators uniformly cause prey to engage in antipredator behaviour. Both perspectives draw on empirical examples to support their respective assumptions. This then raises the question: what direct and indirect effects do different predators have on the same food webs? This question cannot be answered by comparing studies involving single predators and prey because prey responses to predators may be contingent on environmental conditions unique to a particular study site. To avoid confounding effects of study site, one must use studies that explicitly examine effects of several predator species on the same prey in a single system (Sih *et al.* 1998).

The few studies that explicitly examined indirect effects of different predators in the context of food web interactions revealed that the nature of the indirect effects seem to be related to the specific identity of the predator. In a stream system, brook trout (*Salvelinus fontenalis*) and stonefly (*Megarcys signata*) are both active hunters but trout prowl the water column whereas stoneflies crawl on the stream bottom. Mayfly (*Baetis bicaudatus*) prey avoided contact with trout by hiding under rocks and becoming inactive and mayflies avoided stoneflies by drifting away to other locations (Peckarsky & McIntosh 1998). These

differential responses of mayflies to predators altered the extent and spatial distribution of mayfly impacts on their algal food resources. In a pond system (Bernot & Turner 2001), pumpkinseed sunfish (*Lepomis gibbosus*) and crayfish (*Orconectes rusticus*) hunt *Physa* snails. Pumpkinseed are active hunters that continually prowl the water column whereas crayfish wait for prey at a fixed location and ambush them whenever they approach within striking distance. When faced with predation risk from pumpkinseed, snails sought covered habitats; when faced with predation risk from crayfish, snails moved to the surface of the water (Bernot & Turner 2001). Consequently, sunfish caused a reduction in periphyton biomass in covered habitats and an increase in periphyton in the snail's normal open-water habitat. Crayfish presence caused reductions in near-surface periphyton, and increases in periphyton in the normal snail habitat. In a New England old-field system, the generalist grasshopper *M. femurrubrum* faces risk from three spider species (Schmitz & Suttle 2001). *P. mira* is a steadfastly phliopatric sit-and-wait predator in the upper canopy of the field. *Phidippus rimator*, like pumpkinseed sunfish in the pond system, actively hunts its prey throughout the entire old-field canopy. *Rabidosa rabida* is a sit-and-pursue hunter in the lower canopy and on the ground, and like the crayfish, it waits for prey at a fixed location and rushes out to ambush them. Grasshoppers shift their habitat use from grasses to herbs in the presence of the comparatively sedentary *P. mira* and *R. rabida*, relative to a no predator control, but do not change their behaviour in the presence *P. rimator* (Schmitz & Suttle 2001). *P. mira* had a positive indirect effect on grass and a negative indirect effect on herbs. There was no net difference in grasshopper density between the predation treatment and the no predator control. Thus, the cascade was wholly a TMII (Schmitz & Suttle 2001). In addition to causing a habitat shift, *R. rabida* significantly reduced grasshopper density relative to a no-predator control that in turn led to a positive indirect effect on both grasses and herbs – a DMII. In this case, the density effects of the predator swamped out the behavioural effects. Finally, *P. rimator* caused a significant reduction in grasshopper density relative to a no-predator control that also led to a positive DMII on both grasses and herbs.

Different prey in the same system may respond differently to the same predator leading to different community structure. Herbivorous minnows (*Campostoma anomalum*) and crayfish (*O. virilis*) differ in their avoidance of bass (*Micropterus salmoides*) predators thereby changing the nature of the TMII (Gelwick 2000). Bass congregate within specific pools and minnows avoid those pools. Crayfish avoid bass by feeding at night when bass are inactive and hide in burrows during daytime. Predators have a positive and negative indirect effect on algae by causing minnows to move out of pools and damage algae in refuges; predators have a positive indirect effect on algae by causing crayfish to reduce foraging.

Thus, predator species elicit different risk responses in a prey species. In certain cases there is no evident behavioural response, as is assumed by classical theory in population ecology. In other cases, there is activity reduction and/or habitat shift, as is assumed by contemporary theory on trait-mediated effects.

Predator (taxonomic) identity may however simply be a surrogate for other ecological characteristics of the predators – namely their hunting mode (sit-and-wait, active, etc.) (Schoener 1971; Schmitz 2003b) and their habitat domain, defined as the portion of the entire habitat used by the predator relative to that of the prey (Schmitz 2003b). Predator species can be classified according to three hunting modes (Schmitz 2003b). (1) Sit-and-wait in which an ambush predator remains at a fixed location for prolonged periods whether it is hunting or not (days to weeks). (2) Sit-and-pursue where the predator remains at a fixed feeding location and rushes at and pounces on prey when they are in the predator's vicinity. These predators move to new feeding locations when the prey becomes scarce. (3) Active hunting predators that are continuously on the prowl seeking prey. A synthesis of multiple predator studies with such hunting modes in mind (Schmitz 2003b) revealed that habitat domain determines the nature of the prey response to predators and predator hunting mode determines whether effects of antipredator behaviour of prey persist or attenuate at the community level (Fig. 2), that is, whether TMII or DMII dominate. Whenever, prey and predator occupy the same portion of the entire habitat (each

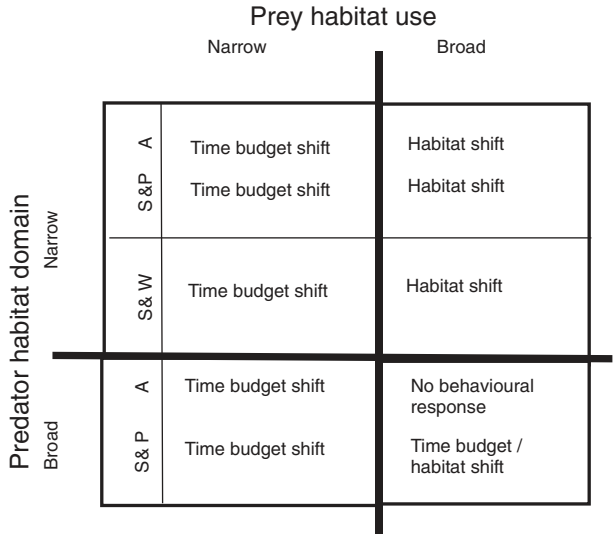

Figure 2 Synthesis of prey antipredator responses in relation to prey and predator habitat domain and predator hunting mode. S & P, A and S & W are sit-and-pursue, active and sit-and-wait hunting strategies, respectively. Species with a narrow habitat domain select only part of the entire available habitat. Species with a broad habitat domain use the entire range of habitat.

have a narrow domain), prey routinely respond with chronic predator evading behaviour (Fig. 2). Likewise, prey with a narrow habitat domain that face widely roaming predator (broad habitat domain) have no recourse but to reduce conspicuous activity when that predator is in the prey's habitat (Fig. 2). Prey that use a variety of habitats (broad domain) undergo habitat shift when facing predators with a narrow habitat domain (Fig. 2). Finally, when prey and predators both have broad habitat domains, they rarely exhibit habitat shifts or activity reductions (Fig. 2).

The above takes a strongly prey-centric perspective on predator-prey interactions. However, predators are also known to adjust their hunting modes and habitat domains in response to changing environmental conditions, physiological state and prey antipredator behaviour (Lima 2002). Broad empirical evidence for cascading effects resulting from altered predator-hunting strategies in response to prey antipredator behaviour remains non-existent (Lima 2002). We know of one case in which altered predator hunting behaviour has been shown to alter both the nature and strength of the cascading effects. On Isle Royale, Michigan interactions among wolves (*Canis lupus*), moose (*Alces alces*), and balsam fir (*Abies balsamea*) are linked to winter snowfall levels. Whenever snowfall levels are high, wolves hunt in larger packs than in low snowfall winters and they prey on moose that tend to aggregate along lakeshores because they are encumbered elsewhere by deep snow (Post *et al.* 1999). Wolves are extremely efficient at killing moose in these conditions because moose have little recourse to escape once encountered. Thus wolves reduce moose populations to levels where they cause limited damage to balsam fir – largely a DMII. In years when snowfall levels are low, moose scatter more widely across the landscape. In this case, hunting in large packs becomes inefficient, so wolves disaggregate into smaller packs and become more confined to local territories (Post *et al.* 1999). Moose population density remains high in these years because moose more freely escape predation by fleeing (Post *et al.* 1999) or by seeking refuge habitats (Edwards 1983). This then leads to a stronger impact of moose on balsam fir than in high snowfall years (Post *et al.* 1999). The ability of moose to evade wolves, in this case, ultimately leads to lower predation mortality and in turn larger effects on balsam fir across the landscape – largely a TMII.

THE PRIMACY OF TRAIT-MEDIATED INDIRECT INTERACTIONS: A HYPOTHESIS

The fact that a single prey species responds differently to different predator species or predator behaviour suggests that prey can discriminate among predator-specific threats. Different predator avoidance behaviour of prey may then represent different degrees of risk aversion resulting from the amount of information prey have about predators (Bouskila & Blumstein 1992; Sih 1992). Predators that are continuously present within a specific habitat domain may provide persistent cues to prey in those locations. So habitat shift or activity reduction is warranted. Alternatively, active predators with broad habitat domains may provide persistent cues throughout the entire habitat forcing prey to weigh a considerable energetic and survival penalty associated with a continuous response against the likelihood of encountering and being captured by the predator at any one time period. Prey facing highly mobile predators may be the least risk averse, considering the fitness costs associated with continuous predator avoidance (Bouskila 2001). Thus, there is a continuum of ways that a prey species responds to different predator species. The exact response ultimately is determined by the costs and benefits of responding to predators with particular hunting modes and habitat domains. Fundamentally then, there is a flexible interplay between predators and prey (Sih 1984; VanBaalen & Sabelis 1993; Brown *et al.* 1999; Bouskila 2001; Kotler *et al.* 2002; Lima 2002; Krivan & Schmitz 2003). A complete picture of the direct and indirect effects of predators in food webs must consider an interplay that transcends several levels of ecological organization – the individual, population and community.

This leads to the hypothesis that ultimately trophic cascades are determined by behavioural responses of prey to predators with different hunting modes and habitat domains (Fig. 3). Sit-and-wait predators should cause prey mortality

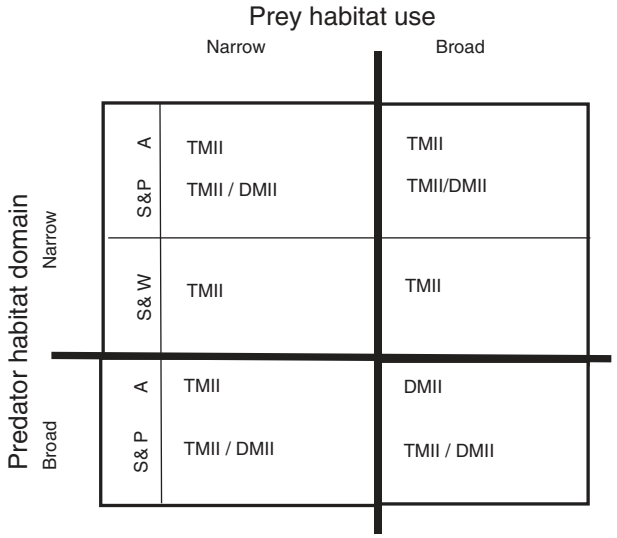

Figure 3 Hypothesized nature of emergent trophic cascade in cases involving different prey behavioural responses to predators with different hunting modes and habitat domains. S & P, A and S & W are sit-and-pursue, active and sit-and-wait hunting strategies, respectively. Species with a narrow habitat domain select only part of the entire available habitat. Species with a broad habitat domain use the entire range of habitat.

that is compensatory to natural mortality (i.e. no net additive effect on prey density) and thus TMIIs will tend to dominate (e.g. Beckerman *et al.* 1997; Gastreich 1999). Actively hunting predators with broad habitat domains should generally cause DMIIs to dominate whenever prey have a broad habitat domain (e.g. Schmitz & Suttle 2001). Alternatively, TMIIs likely will emerge when predators have a broad habitat domain and prey have a narrow habitat domain (Schmitz 2003b). Active predators with a narrow habitat domain should cause TMIIs regardless of prey habitat domain (e.g. Power *et al.* 1985; McIntosh & Townsend 1996; Turner 1997; Peckarsky & McIntosh 1998). Finally sit-and-pursue predators should cause a mixture of TMII and DMII (e.g. Schmitz & Suttle 2001). Whichever dominates depends on the ability of prey to detect and either avoid or escape from their predators.

Future research

This hypothesis argues for greater effort to unmask trait effects and quantify their relative importance in different systems (Werner & Peacor 2003). Indeed, many predator species exhibit sit-and-pursue strategies (Schmitz 2003b). Thus there may be a rich amount of interaction between trait and density effects in many systems. Studies aiming to unmask trait effects should include three elements. First, behavioural responses of prey to predators should be measured in experiments where predators are prevented from killing prey. Second, the survivorship of prey should be measured in the presence and absence (predation control) of predators. Ideally, such a study should include treatments that measure prey survival as a consequence of risk alone and predation alone to tease apart behavioural and density effects on population demography (Peacor & Werner 2001). Finally, the indirect effect of the predator on the prey's resource should be measured over the long-term to elucidate the strength and nature of the indirect effect. This should again be carried out by including both risk-only and predation treatments to allow comparison of TMII and DMII.

CONCLUSIONS

Ecologists are struggling to understand and predict food web interactions in heterogeneous environments (Hunter & Price 1992; Persson 1999; Polis 1999). The challenge is to identify a unifying conceptualization of food web interactions that accounts for the flexible responses species display in the face of changing abundances of resources and predators. We suggest a powerful conception is to view ecological systems as 'landscapes of fear' (Brown *et al.* 1999) in which all indirect effects are ultimately trait-based. Different predators just create different rules of engagement based on their hunting mode and habitat domain. These different rules then determine whether TMII or DMII emerge at the population and community level.

A TMII conceptualization is increasingly being applied to cases of biological control (Janssen *et al.* 1998; Snyder & Wise 2000), conservation of marine ecosystems (Dill *et al.* 2003) and restoration of alpine aspen parkland ecosystems (Ripple *et al.* 2001). Further, concerted efforts to elucidate the interplay between density and trait effects should provide the insight needed to explain variation in the nature and strength of trophic cascades among ecosystems for both basic ecological understanding and applications to management.

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