# CONSUMPTIVE AND NONCONSUMPTIVE EFFECTS OF PREDATORS ON METACOMMUNITIES OF COMPETING PREY

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*Abstract.* Although predators affect prey both via consumption and by changing prey migration behavior, the interplay between these two effects is rarely incorporated into spatial models of predator–prey dynamics and competition among prey. We develop a model where generalist predators have consumptive effects (i.e., altering the likelihood of local prey extinction) as well as nonconsumptive effects (altering the likelihood of colonization) on spatially separated prey populations (metapopulations). We then extend this model to explore the effects of predators on competition among prey. We find that generalist predators can promote persistence of prey metapopulations by promoting prey colonization, but predators can also hasten system-wide extinction by either increasing local extinction or reducing prey migration. By altering rates of prey migration, predators in one location can exert remote control over prey dynamics in another location via predator-mediated changes in prey flux. Thus, the effect of predators may extend well beyond the proportion of patches they visit. In the context of prey metacommunities, predator-mediated shifts in prey migration and mortality can shift the competition–colonization trade-off among competing prey, leading to changes in the prey community as well as changes in the susceptibility of prey species to habitat loss. Consequently, native prey communities may be susceptible to invasion not only by exotic prey species that experience reduced amounts of mortality from resident predators, but also by exotic prey species that exhibit strong dispersal in response to generalist native predators. Ultimately, our work suggests that the consumptive and nonconsumptive effects of generalist predators may have strong, yet potentially cryptic, effects on competing prey capable of mediating coexistence, fostering invasion, and interacting with anthropogenic habitat alteration.

*Key words: behavior; competition; consumptive effects; habitat loss; invasion; metacommunity; metapopulation; migration; nonconsumptive effects; predator–prey interactions.*

## INTRODUCTION

Spatial dynamics affect the persistence of populations (Levins 1969, Hanski and Gilpin 1997), alters the outcome of competition (e.g., the competition–colonization trade-off [Nee and May 1992, Tilman 1994, Amarasekare 2003]), mediates the stability of predator–prey interactions (Holt 1997, Melian and Bascompte 2002, Mouquet et al. 2005), and thus has important implications for ecological invasions (Fagan et al. 2002) and conservation, e.g., minimum viable metapopulations (Hanski et al. 1996). Recently, the emerging paradigm of metacommunity dynamics has stressed the interplay between spatial dynamics and interactions among species (Holyoak et al. 2005). Colonization and extinction are key parameters of both metapopulation and metacommunity dynamics (Hanski and Gilpin 1997, Holyoak et al. 2005). Although often treated as fixed and intrinsic in metacommunity models (Mouquet et al. 2005), substantial evidence suggests that colonization and extinction are subject to alteration by biotic interactions (Wooster and Sih 1995, Reed and Levine 2005, Resetarits et al. 2005). Such interaction-mediated changes in extinction and colonization are likely to be especially relevant in the context of metacommunities, because metacommunities explicitly contain multiple species (Holyoak et al. 2005).

Predators are likely to affect prey colonization and extinction by consuming prey ("consumptive effects") as well as by causing changes in prey activity, behavior, and development ("nonconsumptive effects"; see Plate 1); empirical data suggest that both effects are important components of predator–prey interactions (Werner and

PLATE 1. *Drunella doddsi* (Ephemeroptera: Ephemerellidae) is one of several invertebrate predators on *Baetis bicaudatus* (Ephemeroptera: Baetidae) in Rocky Mountain streams of western Colorado, USA. Other invertebrate predators include stoneflies (Plecoptera) and caddisflies (Trichoptera). *Baetis* has evolved numerous behaviors and life-history strategies to reduce consumption by both invertebrate and vertebrate (Salmonidae) predators, resulting in non-consumptive effects on prey fitness that often exceed those of consumption (Peckarsky and McIntosh 1998). Photo credit: A. McIntosh.

Hall 1988, Lima and Dill 1990, Brown et al. 1999, Werner and Peacor 2003, Preisser et al. 2005, Stankowich and Blumstein 2005). Metacommunity models of consumptive effects (Holt 1997, Nee et al. 1997, Bascompte and Sole 1998, Diehl et al. 2000, Swihart et al. 2001, Melian and Bascompte 2002) have shown that predator-mediated changes in prey extinction can have important consequences for the dynamics of specialist predators and their prey. In the metacommunity context, a key nonconsumptive effect involves the influence of predators on prey movement and migration. For example, predators may alter prey colonization via habitat selection (Krivan and Sirot 2002, Resetarits et al. 2005, Abrams et al. 2007) or by dispersal behavior (Sih and Wooster 1994, Wooster and Sih 1995, Reed and Levine 2005). To this end, a handful of metacommunity models have examined how predator-mediated changes in prey behavior affect the dynamics between specialist predators and a single prey species (Holt 1997, Diehl et al. 2000, Prakash and de Roos 2002). These studies have shown that the nonconsumptive effects of specialist predators on single prey species can be counterintuitive, such as potentially promoting prey abundance and persistence (e.g., Prakash and de Roos 2002, Reed and Levine 2005).

When extended to include predators and competing prey (Holt 1997, Melian and Bascompte 2002), metacommunity models clearly demonstrate that the spatial dynamics of predator and prey can alter the nature of metacommunity dynamics. In these models, prey compete indirectly via apparent competition (Holt 1997, Melian and Bascompte 2002) and asymmetrical intraguild predation (Melian and Bascompte 2002), and their

dynamics are driven by specialist predators explicitly linked to prey populations. Taken together, these models suggest that predator-mediated changes in prey migration can alter prey dynamics, and predators can alter the outcome of interactions among indirectly competing prey. Given the theoretical importance of predator-mediated shifts in colonization for single prey species dynamics, and the prevalence of empirical evidence for nonconsumptive alteration of prey migration, a framework is clearly needed to unify spatial dynamics and the consumptive and nonconsumptive components of predator-mediated shifts in competitive dynamics.

We extend previous metacommunity models of predator–prey dynamics by incorporating both consumptive and nonconsumptive effects of predators. Our work is a departure from previous models in that it incorporates both consumptive and nonconsumptive effects among prey as well as direct competition among prey for patches of habitat. We model generalist predators whose dynamics are not dependent upon the prey they consume. We use this approach because such generalist predators may constitute the bulk of predator biomass in many systems (Sih et al. 1985, Holt and Lawton 1994, Swihart et al. 2001), suggesting that their consumptive and nonconsumptive effects may be important for affecting the dynamics of competing prey.

First, we develop a model of spatial interactions among generalist predators and a single prey species. Upon this foundation, we add competitive interactions among prey to examine how predator-mediated changes in prey colonization and extinction affect the dynamics of prey metacommunities. Finally, we extend our model

to examine how habitat destruction affects prey communities subjected to generalist predators. We show that generalist predators can alter the dynamics of prey extinction and persistence, change the outcome of competition among prey, and interact with anthropogenic ecological change to yield unexpected shifts in prey communities.

## MODELS OF CONSUMPTIVE AND NONCONSUMPTIVE EFFECTS

### Generalist predators and metapopulation dynamics of a single prey species

Consider a prey species where prey populations occupy a proportion, $p$, of all available patches in the landscape, such that the dynamics of the basic model are

$$dp/dt = cp(1 - p) - ep. \quad (1)$$

The basic dynamics of the prey population are dictated by the rate at which populations experience extinction, indicated by $e$, and the rate at which new populations are created by colonization, indicated by $c$. At equilibrium, the proportion of occupied patches is found by setting Eq. 1 equal to zero and solving for $p$, producing

$$p^* = 1 - e/c. \quad (2)$$

This basic model is often referred to as a metapopulation model because of its use by Levins (1969) to describe the dynamics of multiple connected populations. It has also been used as an individual-based model to demonstrate the dynamics of populations (Tilman 1994, Tilman et al. 1997) and as a multispecies spatial competition model (Tilman 1994, Loehle and Li 1996, Tilman et al. 1997). The model has been extended to examine the metapopulation consequences of prey behavior (Smith and Peacock 1990, Ray et al. 1991, Prakash and de Roos 2002), as well as metacommunity competition (Hastings 1980, Nee and May 1992) and trophic dynamics (Holt 1997, Bascompte and Sole 1998, Swihart et al. 2001, Prakash and de Roos 2002). The stability of this basic model, and many of its variants, has been repeatedly demonstrated both analytically and via simulation (e.g., Tilman 1994, Tilman et al. 1997, Swihart et al. 2001). Evaluating the Jacobian matrix of our model under the most complex conditions (Eqs. 8 and 9) also demonstrates that, where it exists, the two-species equilibrium is stable as judged by the Routh-Hurwitz criterion (May 2001).

Our model makes several assumptions that are common to metapopulation and metacommunity models (e.g., Nee and May 1992, Nee et al. 1997). All existing patches are assumed to be habitable by both predators and prey. We assume that encounters between predators and prey are random, and the distribution and abundance of predators is independent of the distribution and abundance of prey. This is a realistic assumption from the predator's perspective, as natural enemies may rarely have perfect information regarding the whereabouts of

prey (Stephens and Krebs 1986, Swihart et al. 2001) and may not be spatially aggregated near prey (Walde and Murdoch 1988). Moreover, a review of empirical studies suggests that foragers often encounter their prey at random (Stephens and Krebs 1986). Although random encounter could largely be generated by widely moving prey, the dynamics in our model are likely to most resemble systems where predators effectively visit a random patch in each instantaneous timestep of the model. (Otherwise, the probability of encountering a predator is not strictly constant per timestep.) Treating predator dynamics as independent of prey dynamics also implies that the abundance of predators is constrained by factors other than the focal prey, or that the abundance of predators changes much more slowly than the abundance of prey, an assumption frequently made in predator–prey models that focus on prey dynamics (e.g., Holt 1987). This assumption is realistic under several common scenarios, for example, if numerical responses of predators occur slowly due to long predator generation time, if predators are limited by spatial constraints, interactions with other predators, or if predators are such generalists that focal prey provide a negligible contribution to predator population growth rate. As in other metapopulation models of predators and prey, we assume that predator-mediated changes in prey colonization and extinction do not covary, although we discuss situations where this might occur in the interest of stimulating future research (see *Discussion*).

To incorporate generalist predators into the model, we assume that a predator visits some proportion of all patches, $b$, in the available landscape. To integrate the effects of predators on prey migration, we use $r$ to denote changes in prey colonization caused by predators and $m$ to denote changes in prey extinction in patches where predators and prey coincide:

$$\frac{dp}{dt} = cp(1 - b)(1 - p) - ep(1 - b) \quad (3a)$$

$$+ (c + r)pb(1 - p) - (e + m)pb. \quad (3b)$$

Eq. 3a represents the dynamics of patches where predators are not present, while Eq. 3b represents the dynamics of patches where predators and prey interact, with prey colonization rates changed by $r$ and prey extinction rate changed by $m$ when prey are in patches with predators. The value of $r$ can be positive or negative because predators may either encourage or discourage prey migration (Lima and Dill 1990, Sih and Wooster 1994, Wooster and Sih 1995, Peckarsky and McIntosh 1998, Reed and Levine 2005). When $r > 0$, predators increase likelihood that prey will disperse from the current patch, thereby increasing the likelihood that they will colonize a new patch. When $r < 0$, predators reduce colonization of patches by prey. This could occur if predators decrease prey migration by discouraging prey movement or by consuming prey that would otherwise migrate, or if prey are less likely to colonize patches that

already contain predators (Resetarits et al. 2005). The value of $m$ is always positive ($m > 0$), because the likelihood that the prey population will go extinct is increased in the presence of a predator (i.e., we assume that predators do not increase survival of prey; see Holt [2002] for an example where predators may increase prey survival). The equilibrium patch occupancy of prey is found by setting Eq. 3 equal to zero and solving for $p$:

$$p^* = 1 - \frac{e + bm}{c + br}. \qquad (4)$$

As this model demonstrates, the total number of patches occupied by prey is a function of prey colonization and prey extinction, as well as the proportion of patches occupied or patrolled by predators ($b$) and predator-mediated changes in prey colonization ($r$) and extinction ($m$). Because of prey movement, patches without predators are under some degree of influence by predator-containing sites (Fig. 1) as long as predators are present in some sites ($b > 0$) and predators have some impact on local prey extinction ($m > 0$). Furthermore, when $e/c > 1 > (e + bm)/(c + br)$, predators are necessary for prey persistence in the landscape. As expected, when predators are not present ($b = 0$) or there is no change in prey migration ($r = 0$) and no change in prey extinction ($m = 0$), the equilibrium is identical to Eq. 2.

### Adding competition to the basic model

The basic model can be extended to examine the effects of predators on competitive interactions among prey by incorporating the approach used by Tilman (1994), as applied to metacommunities (e.g., Nee et al. 1997). Consider two prey species, where species 1 is a superior competitor that displaces species 2 from any patch. Because species 1 can occupy all patches, its dynamics are described by Eq. 3. The dynamics of species 2 require additional terms because patches containing species 1 are not usable by species 2. The dynamics of the inferior competitor (species 2) are

$$\frac{dp_2}{dt} = c_2 p_2 (1 - b)(1 - p_1 - p_2)$$

$$+ (c_2 + r_2)p_2 b(1 - p_1 - p_2) \qquad (5a)$$

$$- e_2 p_2 (1 - b) - (e_2 + m_2)p_2 b \qquad (5b)$$

$$- c_1 p_1 (1 - b)p_2 - (c_1 + r_1)p_1 b p_2 \qquad (5c)$$

where Eq. 5a represents how the dynamics of species 2 are affected by the colonization of new patches, Eq. 5b represents how loss of occupied patches affects the dynamics of species 2, and Eq. 5c represents the loss of patches of species 2 when a patch with species 2 is colonized by the superior competitor (species 1). Generalist predators affect each of these components whenever predators and prey coincide and $r \neq 0$ or $m > 0$. For simplicity, we assume that the encounter rate of the
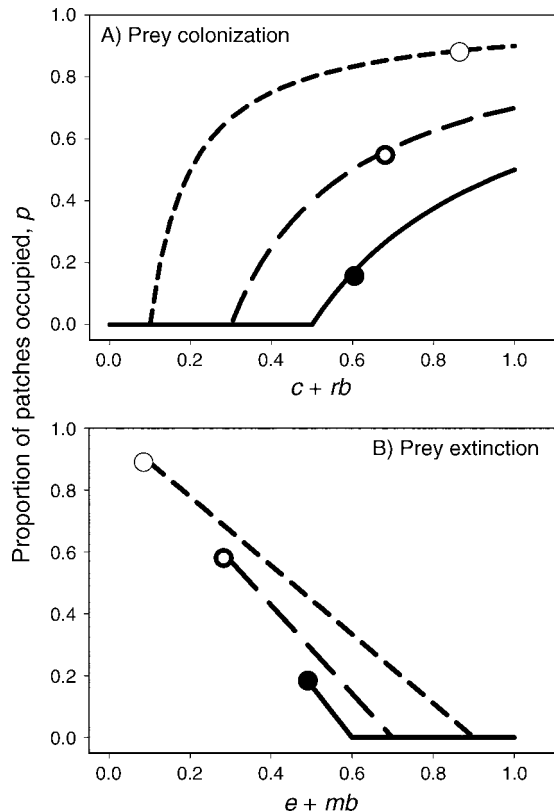


FIG. 1. Metapopulation consequences of generalist predators. Each line represents a metapopulation with a different equilibrium size in the absence of effects of predators, where $c$ is the rate at which prey colonize empty patches, and $e$ is the rate at which prey populations go extinct. Generalist predators present in a proportion, $b$, of patches can affect prey by increasing prey mortality by amount $m$ or altering prey colonization by amount $r$. Solid lines represent a small metapopulation ($c = 0.6$, $e = 0.5$), medium-dashed lines represent a medium-sized metapopulation ($c = 0.7$, $e = 0.3$), and short dashes represent a large metapopulation ($c = 0.9$, $e = 0.1$). Circles correspond to the equilibrium realized when predators are absent (i.e., $b = 0$) or there are no consumptive or nonconsumptive effects of predators (i.e., $r = 0$, $m = 0$), identical to the equilibrium obtained with the Levins model. In (A) and (B) the product of predator abundance ($b$) and the effect of predators on prey ($r$ or $m$) are presented. This is because predators that are very common with weak effects are predicted to have the same effect on prey as rare predators that have very strong effects (e.g., $rb = 0.16$ when $b = 0.8$ and $r = 0.2$ and when $b = 0.1$ and $r = 1.6$). (A) The influence of predator-mediated changes in prey colonization ($r$) at different values of predator patch occupancy ($b$). (B) The influence of predator-mediated changes in prey extinction ($m$) at different values of predator patch occupancy.

predator and each prey is determined solely by the relative proportion of patches occupied by each prey species. Although not explored here, considering the outcome of competition under different encounter scenarios (e.g., if predators aggregate in patches with a particular prey type) would be a worthwhile avenue for future research.

As defined, the equilibrium patch occupancy of the superior competitor (species 1) is unaffected by compe-

## A) Rare predator (b = 0.1)
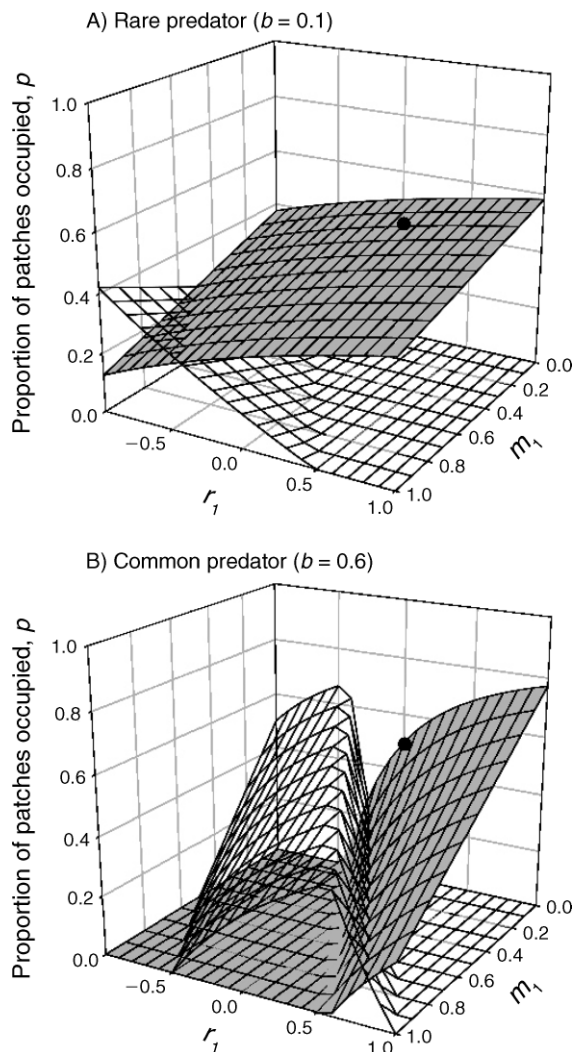


## B) Common predator (b = 0.6)



FIG. 2. The effect of generalist predators on the outcome of metacommunity competition among a superior competitor (gray plane; species 1) and an inferior competitor (clear plane; species 2). Panels indicate how the impact of predators might differ between the two competitors that differ in how they are affected by generalist predators. The effect of the generalist predator on the inferior competitor is half as strong as the predator's effect on the superior competitor (i.e., $m_2 = m_1/2$; $r_2 = r_1/2$). Dots correspond to the equilibrium of species 1 realized when there is no effect of predators; under these conditions, species 2 is always excluded.

tition from species 2, and is described by Eq. 4. The equilibrium patch occupancy of species 2 is

$$p_2^* = 1 - \frac{e_2 + bm_2}{c_2 + br_2} - \left[ p_1^* \left( 1 + \frac{br_1 + c_1}{br_2 + c_2} \right) \right]. \quad (6)$$

The unbracketed terms in Eq. 6 represent the effect of generalist predators on species 2 in absence of competition from species 1, whereas the bracketed term represents the reduced abundance of species 2 because it cannot inhabit patches that also contain species 1.

Because species 1 always displaces species 2, the relative rate at which species 2 is excluded from patches by species 1 is a function of the colonization rates of each species. In the absence of competition, the minimum requirement for species $i$ to persist is $(e_i + bm_i) < (c_i + br_i)$. To determine the conditions needed for invasion, we evaluate the conditions necessary for $dp_2/dt$ to be positive when the superior competitor is at equilibrium (i.e., $p_1 = p_1^*$). To invade, the inferior invader must have

$$c_2 + br_2 > \frac{p_1(c_1 + br_1)}{1 - p_1} + \frac{(e_2 + bm_2)}{1 - p_1}. \quad (7)$$

As Eq. 7 demonstrates, generalist predators could readily alter the conditions for coexistence (Fig. 2), such that the otherwise inferior competitor could invade. As expected, when there are no generalist predators in the system (i.e., $b = 0$), or predators have no effect on prey ($r_1 = r_2 = 0$; $m_1 = m_2 = 0$), Eq. 7 becomes identical to the standard invasion criterion for predator-free models (Tilman 1994). As Eq. 7 shows, if predators do not affect the colonization of the inferior competitor ($r_2 = 0$), they can still allow the inferior competitor to invade by sufficiently reducing the colonization of the superior competitor (i.e., $r_1 < 0$). The effects of predators on the inferior competitor is also not limited to changes in migration of one or both competitors; as predator-mediated changes in mortality can also guide dynamics (Fig. 2). Importantly, because prey movement can effectively extend the influence of a generalist predator, predators that only affect a fraction of patches in the landscape (i.e., $b$), at any given time could lead to landscape-wide shifts in the entire competitor community by altering $r$, $m$, or both.

### Incorporating habitat destruction

The models presented above assume that all patches in the landscape are usable habitat for prey in the absence of competitors. However, anthropogenic habitat destruction may reduce the proportion of patches habitable by prey in the landscape. To determine how habitat destruction might affect competition among prey in our model, we use $D$ to represent the proportion of total habitat that is permanently destroyed. Prey that land within destroyed patches are lost from the system, an approach consistent with other metapopulation models that incorporate habitat destruction (e.g., Nee and May 1992, Nee et al. 1997, Bascompte and Sole 1998). We assume that destruction does not alter the proportion of patches with prey visited by generalist predators. The dynamics of species 1 are described by

$$\frac{dp_1}{dt} = c_1 p_1 (1 - b)(1 - D - p_1)$$

$$+ (c_1 + r_1) p_1 b (1 - D - p_1) \quad (8a)$$

$$- e_1 p_1 (1 - b) - (e_1 + m_1) p_1 b \quad (8b)$$

and the dynamics of species 2 are described by

$$\frac{dp_2}{dt} = c_2 p_2 (1 - b)(1 - D - p_1 - p_2)$$

$$+ (c_2 + r_2) p_2 b (1 - D - p_1 - p_2) \quad \text{(9a)}$$

$$- e_2 p_2 (1 - b) - (e_2 + m_2) p_2 b \quad \text{(9b)}$$

$$- c_1 p_1 (1 - b) p_2 - (c_1 + r_1) p_1 b p_2. \quad \text{(9c)}$$

The net effect of habitat destruction is to reduce the conditions for persistence, such that equilibrium patch occupancy of species 1 becomes

$$p_1^* = 1 - D - \frac{(e_1 + bm_1)}{(c_1 + br_1)} \quad \text{(10)}$$

and the equilibrium patch occupancy of species 2 becomes

$$p_2^* = 1 - D - \frac{(e_2 + bm_2)}{(c_2 + br_2)} - \left[ p_1^* \left( 1 + \frac{br_1 + c_1}{br_2 + c_2} \right) \right]. \quad \text{(11)}$$

These models demonstrate that the susceptibility of any particular prey species to habitat destruction is a function of basic prey traits ($c$ and $e$) as well as a function of the consumptive and nonconsumptive effects of generalist predators. Thus, species 1 goes extinct when $D > 1 - [(e_1 + bm_1)/(c_1 + br_1)]$, and species 2 goes extinct when

$$D > 1 - \frac{(e_2 + bm_2)}{(c_2 + br_2)} - \left[ p_1^* \left( 1 + \frac{br_1 + c_1}{br_2 + c_2} \right) \right]. \quad \text{(12)}$$

Because superior competitors are expected to have lower levels of colonization under the competition–colonization trade-off (Nee and May 1992, Tilman 1994, Nee et al. 1997), these species will be the first to experience extinction as habitat is destroyed; i.e., at lower levels of $D$ (Nee and May 1992, Nee et al. 1997, Tilman et al. 1997). Therefore, under the competition-colonization trade-off, extinction of species 2 may occur when $D > 1 - [(e_2 + bm_2)/(c_2 + br_2)]$, because the bracketed term in Eq. 12 will equal zero when species 1 is extinct. Once $D$ is surpassed for a particular prey species, extinction is deterministic, a condition known as the Levins Rule (Hanski et al. 1996).

## DISCUSSION

Our results suggest that the influence of predators on the dynamics of prey may be more pervasive than generally appreciated. By changing prey migration and the likelihood of local extinction, predators can alter the dynamics of prey metapopulations (Fig. 1), even when predators only inhabit a small fraction of patches at once. Moreover, the effect of predators extends to competition within prey metacommunities: by changing rates of colonization and extinction, predators can shift the nature of the competition–colonization trade-off that leads to system-wide extinction or persistence of inferior competitors. This has implications for metacommunity paradigms based on competition (e.g., mass effects, species sorting), but also for metacommunity paradigms where competition among prey is nonexis-

tent. For example, generalist predators might affect prey metacommunities characterized by neutral dynamics simply by altering rates of prey patch colonization (i.e., $c + br$) and extinction (i.e., $e + bm$).

*Generalist predators and metapopulation dynamics of prey*

By consuming and frightening prey, generalist predators are capable of changing the abundance of prey and affecting the stability of prey metapopulations. Prey go extinct whenever $(e + bm) > (c + br)$. Thus, if predators increase prey migration ($r > 0$), the number of sites occupied by prey at equilibrium is increased, even to the extent that generalist predators could lead to the persistence of prey metapopulations that would otherwise go extinct, i.e., where $e/c > (e + bm)/(c + br)$. This outcome has been shown in the context of metapopulation dynamics (Reed and Levine 2005) and specialist predators (Holt 1997, Prakash and de Roos 2002). Our results expand this view to demonstrate that generalist predators are also capable of promoting the persistence of prey metapopulations otherwise destined for extinction, and this can arise via consumptive or nonconsumptive effects. Conversely, when $m > 0$ and $r < 0$, generalist predators could lead to the extinction of otherwise large, stable prey metapopulations, i.e., where $(e + bm)/(c + br) > e/c$. Such an outcome might be particularly likely in situations where introduced generalist predators attack naïve prey that suffer heavy mortality or exhibit maladaptive antipredator responses (A. Sih et al., *unpublished manuscript*).

Our model shows that, although generalist predators may not be everywhere at once (i.e., $b = 1$), their effect on prey may extend beyond sites occupied by predators. This occurs because predator-mediated shifts in prey migration can propagate entirely via prey, giving rise to dynamics at one time and place that are a function of predators elsewhere. This "remote control" (J. L. Orrock et al., *unpublished manuscript*) of prey by predators contrasts with donor control, whereby subsidies of prey from predator-free patches affect predator dynamics, but predators do not affect prey subsidies (Polis et al. 1997). Our model shows that, as long as prey migrate, predators can also influence prey subsidies. For example, the dynamics of fish in predator-free tributaries are a function of predators in connecting streams (Fraser et al. 1999, Gilliam and Fraser 2001); thus predators receive subsidies of prey but also affect the dynamics of prey in remote habitats.

Our model also suggests that relatively rare predators may nonetheless have dramatic impacts on system-wide dynamics of prey, i.e., some predators may be "keystone intimidators" (Peckarsky et al. 2008). A rare predator that is frightening ($r \gg 0$) or voracious ($m \gg 0$) but only visits a few patches each season (i.e., low $b$) may nonetheless have widespread effects on prey dynamics because sites without predators will still be affected by changes in prey migration from the predator-containing sites. For example, the pea aphid, *Acyrthosiphon pisum*,

can produce either winged or sessile offspring and produces more winged offspring in response to the presence of a lady beetle predator. Even though lady beetles are highly mobile and rarely spend more than a few hours on plants, a short visit by lady beetles results in the production of more winged morphs 7–8 days following the predator encounter (Minoretti and Weisser 2000). Thus, even if their visits are short and infrequent, generalist lady beetle predators may influence large-scale aphid population dynamics by inducing shifts in the proportion of dispersing (i.e., winged) aphids.

Although we treat them as independent, $r$ and $m$ may covary due to trade-offs among prey escape tactics and predator hunting abilities. For example, when prey reduce migration in the presence of predators ($r < 0$), this is also expected to reduce the likelihood that prey will be consumed by predators ($m$ approaches zero). That is, reducing migration or remaining stationary reduces the likelihood of encountering a predator during migration and may promote escape from predators that hunt using prey motion. Our model shows that, assuming $c > e$, prey that respond to heavy predation pressure by large increases in migration will persist as long as $m$ and $r$ are equal in magnitude and opposite in sign (i.e., $r + m = 0$). The prediction that prey that experience heavy mortality from a predator should exhibit large shifts in migration whenever predators are near is in agreement with models from foraging theory (Stephens and Krebs 1986). Covariance between $r$ and $m$ could also arise when emigration from a patch increases the likelihood of patch extinction, because the likelihood of extinction is likely to change with prey population size. The relative degree to which changes in $r$ affect overall abundance of prey is also dependent upon the availability of sites available to be colonized by prey, i.e., positive changes in $r$ are less important in changing prey abundance once prey already inhabit a large fraction of open sites (Fig. 1). Conversely, predator-mediated changes in $r$ and $m$ may be particularly important in affecting the persistence of prey when many open sites exist in the landscape. Although not examined in our model, differences in prey emigration and immigration behavior are also likely to affect the magnitude of predator-mediated dynamics. For example, if predators increase the likelihood that prey will leave a patch (i.e., $r > 0$), and mobile prey are also unlikely to settle in patches that contain predators (Resetarits et al. 2005), the effect of predators in altering the flux of prey into predator-free patches may be even greater than our model predicts.

### Generalist predators and competing prey

In models that treat patches as homogenous, coexistence among multiple species is possible as long as inferior competitors are superior colonists (Mouquet et al. 2005). The importance of predator-mediated changes in density and resource competition has been examined in nonspatial models (Holt et al. 1994); we demonstrate that predators may alter this relationship in space,

creating heterogeneous prey dynamics in otherwise homogeneous patches. Moreover, we show that the impact of predators is not limited to predator-mediated changes in prey extinction (Fig. 2); the competition–colonization trade-off can be altered by predator-mediated changes in prey dispersal behavior. Predators may thus be requisites for coexistence, but predators may also become a mechanism of competitive exclusion via their consumptive or nonconsumptive effects on competing prey (Fig. 2). Ultimately, the importance of predator-mediated changes in colonization is likely to be a function of the metacommunity framework that best describes a particular community, i.e., neutral, patch dynamics, mass effects, or species sorting. Changes in colonization caused by predators may be important in metacommunities described by neutral dynamics and patch dynamics because such communities are shaped by patterns of colonization and extinction, and the competition–colonization trade-off, respectively (Chase et al. 2005). Similarly, communities where mass effects are important may also be altered by predator-mediated changes in prey colonization and extinction, whereas communities characterized by species sorting may be least affected by the dynamics of generalist predators.

By extension, the introduction or loss of generalist predators may be capable of shifting the underlying mechanism of metacommunity control, because the four models of metacommunity dynamics vary with regard to the influence of local extinction and colonization. For example, systems that are controlled by species sorting in the absence of predators may become strongly controlled by mass effects if predators arrive and dramatically alter prey migration. In this regard, our model illustrates that field studies must be carefully designed with predators in mind, because predators might dramatically affect the structure of prey communities even if predators only inhabit a fraction of the available prey habitat. Studies focusing on only a subset of habitats or predator conditions might not fully observe the mechanisms driving prey dynamics, and might thus conclude that prey species are at a stable competitive equilibrium, when this equilibrium is actually maintained by predator-mediated changes in prey migration and/or mortality.

Our model also illuminates aspects of predator-mediated biological invasions (A. Sih et al., *unpublished manuscript*). The impact of generalist predators on the outcome of competition will be largest when competing prey have very different values of $m$ and $r$, a scenario that may be particularly likely when prey species do not share the same evolutionary history with a common predator (A. Sih et al., *unpublished manuscript*). For example, exotic species may be more likely to invade if predators in the introduced range have greater impacts on native species ($m_{\text{native}} > m_{\text{exotic}}$), analogous to the enemy release hypothesis (Keane and Crawley 2002). Our model adds a novel twist to this concept by demonstrating that native predators might also reduce

migration of native prey, but not affect dispersal of exotic prey that they do not attack, such that $r_{native} < r_{exotic}$, and exotic competitors might thus invade. As such, exotics may benefit from behavioral predator release as well as the mortality-based predator release often associated with invasion. Alternatively, predator-mediated effects could reduce the likelihood of invasion by exotic prey (i.e., biotic resistance), contributing to the general pattern in invasion biology that the vast majority of exotic species fail to become invasive. Regardless of whether exotic prey are better competitors than native prey in the absence of native predators, our model suggests that the consumptive and nonconsumptive impacts of predators may tip the balance and alter the outcome of invasion. Because prey may be more likely to have adaptive responses to predators they have experienced over evolutionary timescales, invasion may be most likely when exotic prey are accompanied by exotic predators (A. Sih et al., *unpublished manuscript*). In this case, whereas exotic prey exhibit values of $r$ that are adaptive given $m$ and $b$, native prey may not recognize the novel predator and may thus exhibit a maladaptive response to the exotic predator (e.g., a value of $r$ that increases the likelihood of predation), and thus suffer greater mortality.

### Habitat destruction

The Levins Rule predicts the degree of habitat destruction required for metapopulation extinction (Hanski et al. 1996); we show that generalist predators can change the dynamics of metapopulation persistence. Under the competition–colonization trade-off, superior competitors are expected to be those with lowest colonization abilities, and thus those most sensitive to habitat loss (Nee and May 1992, Tilman et al. 1997). When applied to metacommunities, our model suggests that prey that experience generalist predators will become extinct whenever $D > 1 - [(e + bm)/(c + br)]$ (see Eq. 10). As a result, in addition to colonization and extinction, predator-mediated changes in prey dispersal behavior and mortality can alter prey susceptibility to habitat loss. When they promote prey dispersal, generalist predators can increase the ability of prey to withstand habitat loss, such that prey incapable of persisting alone can persist when the predator is present. As such, conservation plans that do not account for predator-mediated effects could erroneously conclude that a species has ample habitat to persist, when the species only has ample habitat to persist as long as its generalist predator is also present.

In addition to affecting the amount of habitat lost, $D$, anthropogenic habitat destruction is also capable of altering other model parameters. Habitat destruction may change $c$ by altering connectivity among remaining fragments (Englund and Hamback 2007). By changing the composition and configuration of habitats, landscape alteration may also affect ($b$) the number of patches visited by predators, as well as ($m$) the increase

in mortality caused by predators. Similarly, by affecting structure and permeability, habitat alteration may also change the likelihood ($r$) that prey will disperse. As such, a single-species or single-parameter approach to modeling populations of conservation concern is unlikely to succeed; it is imperative that we understand how anthropogenic habitat destruction and alteration affect predators and prey to effectively conserve species. Similarly, conservation tools that alter dispersal, such as conservation corridors (e.g., Haddad et al. 2003) may also alter metacommunity persistence, especially if an organism's response to a predator depends on the presence of a corridor, as some studies suggest (Brinkerhoff et al. 2005).

Models of habitat loss that incorporate specialist predators whose dynamics are linked with prey demonstrate that there is a trade-off between habitat destruction and prey dynamics. Because predators are generally more affected by habitat loss then their prey, there may be some point at which habitat destruction becomes beneficial for prey by removing predators from the system (Nee et al. 1997, Bascompte and Sole 1998, Swihart et al. 2001). In our model, generalist predators were not explicitly affected by habitat destruction, suggesting that, for prey that are primarily targeted by generalists, habitat loss is unlikely to be beneficial by reducing predator abundance per se. Moreover, habitat alteration may increase the abundance of generalist predators and change the composition of the predator community. For example, large carnivores are often lost from ecological communities due to fragmentation or hunting. If prey metacommunity dynamics are strongly influenced by generalist predators, removal of such fierce, far-roaming generalist predators could reduce equilibrium patch occupancy of prey (i.e., systems where $c + br > e + bm$, but $c < e$). Moreover, the loss of large carnivores is often accompanied by the increase of smaller predators, i.e., mesopredator release (Crooks and Soule 1999). Because mesopredators have very different impacts relative to large predators (i.e., different $m$, $r$, $b$), our model of spatial prey dynamics suggests that anthropogenic changes in the predator community could impact prey in ways that are not intuitively predictable based upon knowledge of only the predator's consumptive or nonconsumptive impacts.

### Conclusions

Our model demonstrates the spatial consequences that arise from the ecology of consumption as well as the ecology of avoiding consumption (e.g., Werner and Hall 1988, Wooster and Sih 1995), such as the ecology of fear (Brown et al. 1999): we show how the interplay of space, dispersal behavior, and consumption affects prey metapopulation dynamics and the composition of prey metacommunities. These dynamics may even arise in predator-free places because predator-mediated shifts in prey can propagate entirely via prey, giving rise to dynamics at one time and place that are a function of

predators somewhere else. Our work, as well as the results of other theoretical (Diehl et al. 2000, Prakash and de Roos 2002) and empirical studies (e.g., Lima and Dill 1990, Wooster and Sih 1995, Peckarsky and McIntosh 1998), suggests that prey dispersal behavior is capable of exacerbating or dampening the effect of predator-mediated mortality. Moreover, we show how consumptive and nonconsumptive effects can lead to changes in competitive exclusion that could alter the structure of prey communities, changing their susceptibility to habitat fragmentation and biological invasion. To fully understand the effect of predators on prey dynamics, future work is needed to generate a robust framework for understanding which factors affect the relative magnitudes of consumptive and nonconsumptive effects. For example, predator-mediated mortality ($m$) is likely to vary as a function of life stage and body size (e.g., gape-limited predators), prey vulnerability, and availability of other prey. Changes in prey colonization caused by predators are likely to vary depending upon the ability of prey to detect and assess risk, costs associated with moving, and density of conspecifics. Although dissecting these components will require careful experimental design and may be logistically difficult, such studies are ultimately the only way to quantify the comprehensive impact of predators within ecological communities.

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