



Effects of Habitat Destruction and Resource Supplementation in a Predator–Prey Metapopulation Model

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We developed a mean field, metapopulation model to study the consequences of habitat destruction on a predator–prey interaction. The model complements and extends earlier work published by Bascompte and Solé (1998, *J. theor. Biol.* **195**, 383–393) in that it also permits use of alternative prey (i.e., resource supplementation) by predators. The current model is stable whenever coexistence occurs, whereas the earlier model is not stable over the entire domain of coexistence. More importantly, the current model permits an assessment of the effect of a generalist predator on the trophic interaction. Habitat destruction negatively affects the equilibrium fraction of patches occupied by predators, but the effect is most pronounced for specialists. The effect of habitat destruction on prey coexisting with predators is dependent on the ratio of extinction risk due to predation and prey colonization rate. When this ratio is less than unity, equilibrium prey occupancy of patches declines as habitat destruction increases. When the ratio exceeds one, equilibrium prey occupancy increases even as habitat destruction increases; i.e., prey “escape” from predation is facilitated by habitat loss. Resource supplementation reduces the threshold colonization rate of predators necessary for their regional persistence, and the benefit derived from resource supplementation increases in a nonlinear fashion as habitat destruction increases. We also compared the analytical results to those from a stochastic, spatially explicit simulation model. The simulation model was a discrete time analog of our analytical model, with one exception. Colonization was restricted locally in the simulation, whereas colonization was a global process in the analytical model. After correcting for differences between nominal and effective colonization rates, most of the main conclusions of the two types of models were similar. Some important differences did emerge, however, and we discuss these in relation to the need to develop fully spatially explicit analytical models. Finally, we comment on the implications of our results for community structure and for the conservation of prey species interacting with generalist predators.

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1. Introduction

Habitat loss and habitat fragmentation (*sensu* Mönkkönen and Reunanen, 1999; With *et al.*,

1997; With & King, 1999) are widespread in natural systems due to anthropogenic changes in land use (e.g., Saunders *et al.*, 1991; Andersen *et al.*, 1996). Changes in the composition and physiognomy of a landscape resulting from habitat loss and fragmentation (Dunning *et al.*, 1992) can

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alter genetic structure (Gaines *et al.*, 1997), individual behavior (Lima & Zollner, 1996; Sheperd & Swihart, 1995), local population dynamics (Nupp & Swihart, 1996, 1998), interspecific interactions (Keyser *et al.*, 1998), and community composition (Dunstan & Fox, 1996; Hecnar & M'Closkey, 1997; Kolozsvary & Swihart, 1999). Not surprisingly, habitat destruction has been implicated as the major threat to biological diversity (Wilcox & Murphy, 1985).

The metapopulation concept provides a useful framework within which to study the implications of habitat loss and fragmentation. A metapopulation is viewed as a network of idealized habitat patches (fragments) in which species occur as discrete local populations connected by dispersal (Hanski, 1998). In its original formulation (Levins, 1969), a proportion p of all patches are occupied, with empty patches being colonized at rate c and occupied patches going extinct at rate e :

$$\frac{dp}{dt} = cp(1 - p) - ep.$$

Under these conditions, the equilibrium proportion of occupied patches, p^* , in a metapopulation is determined by the per patch probabilities of colonization and extinction; i.e., $p^* = 1 - (e/c)$. Of course c and e are influenced by factors intrinsic to the organism under study (e.g., vagility, territoriality, population density, variation in demographic rates) and by factors related to the landscape or patch (e.g., patch isolation, patch area, patch orientation, patch geometry). Generalizations are possible regarding the effects of some of these factors (Fahrig & Paloheimo, 1988; Andr n, 1994; Frank & Wissel, 1998; Wolff, 1999), and considerable progress has been made in modifying the Levins single-species model for predictive purposes in real landscapes (reviewed in Hanski, 1998).

Less attention has been paid to metapopulation models of interacting species, despite the strong likelihood that asymmetric effects of habitat fragmentation could alter dramatically the strength, and perhaps even the type, of interactions. Higher-order effects refer to modified

interspecific interactions which change the abundance, distribution, and persistence of a species (Billick & Case, 1994). Theoretical studies have demonstrated the potential for fragmentation to produce higher-order effects among competitors (Tilman *et al.*, 1994; Moilanen & Hanski, 1995; Nee *et al.*, 1997; Huxel & Hastings, 1998) and predators and prey (May, 1994; Kareiva & Wennergren, 1995; Holyoak & Lawler, 1996; Nee *et al.*, 1997; de Roos *et al.*, 1998).

Habitat loss and fragmentation are of particular concern to conservation biologists in the context of extinction thresholds (With & King, 1999); i.e., nonlinear responses of populations to habitat loss which lead to abrupt declines in patch occupancy over a narrow range of habitat destruction. Few metapopulation models of predator-prey systems have incorporated a component of habitat loss (but see Kareiva & Wennergren, 1995).

Recently, Bascompte & Sol  (1998) formulated a Levins-type metapopulation model to examine the effect of habitat destruction on the dynamics of a prey and its specialist predator. They showed that predators were more sensitive to habitat fragmentation than were prey, and that extinction thresholds for predators were related to predator colonization rate. Although the results of Bascompte & Sol  (1998) are interesting, they did not include an analysis of the stability of the model's equilibria. In addition, many predators in natural systems are not obligate specialists but rather are capable of relying upon other resources to meet their energetic needs. Thus, many predators are capable of resource supplementation (Dunning *et al.*, 1992) to varying degrees, and this may have important implications for the dynamics of a predator-prey system in a fragmented landscape. Herein, we revisit the model of Bascompte & Sol  (1998), pose an alternative formulation, and relax the assumption of extreme specialization by the predator. Specifically, our objectives are to: (1) examine the stability conditions for the model developed by Bascompte & Sol  (1998); (2) formulate an alternative model based on random encounter probabilities of predator and prey; and (3) examine the dynamics of predator and prey under varying conditions of resource supplementation by the predator.

2. The Bascompte and Solé Metapopulation Model

Bascompte & Solé (1998) relied upon a mean field model; i.e., a model depicting behavior in a homogeneous mixing metapopulation composed of an infinite number of local populations. Following May (1994), an additional assumption was that predators were specialists and thus could exist only on patches containing the prey in question. Let x and y represent the proportion of patches occupied by prey and predators, respectively. Then the extension of the Levins (1969) metapopulation model to two trophic levels by Bascompte & Solé (1998) is given as

$$\frac{dx}{dt} = c_x x(1 - x) - e_x x - \mu y,$$

$$\frac{dy}{dt} = c_y y(x - y) - e_y y.$$

Note that the equation for the prey differs from the original Levins (1969) formulation in having an additional term, μy . Bascompte & Solé (1998) added this term to represent the additional extinction risk imposed on prey in patches also occupied by predators. That is, e_x represents the per patch rate of extinction of prey independent of the effect of predators, and μ represents the additional rate of prey extinction due to predators on the fraction of patches (y) in which they co-occur. Thus, the total extinction rate of prey on patches also occupied by predators is $e_x + \mu$. Bascompte & Solé (1998) restricted composite rates for extinction (and colonization) to the interval from 0 to 1, permitting their interpretation as probabilities of occurrence in dt ; we have retained this convention in our paper.

The assumption that predators are specialists capable of surviving only on patches with prey of type X also alters the equation for the predator relative to the original formulation of Levins (1969). Specifically, if some fraction y of patches is occupied by the predator (and, by extension, prey type X), then only a fraction $x - y$ of patches remains available for colonization by the predator.

To model habitat destruction, Bascompte & Solé (1998) introduced a term, D , representing the fraction of sites destroyed and thus unavail-

able for colonization (see also Kareiva & Wennergren, 1995). The resulting model is as follows:

$$\frac{dx}{dt} = c_x x(1 - x - D) - e_x x - \mu y, \quad (1a)$$

$$\frac{dy}{dt} = c_y y(x - y) - e_y y. \quad (1b)$$

Because the predator's occurrence in a patch is conditional on the prey's occurrence there, incorporation of D is only required for the prey eqn (1a). Bascompte & Solé (1998) examined the behavior of this predator-prey model by noting the effect of D , c_y , and μ on the equilibrium fraction of patches containing prey (x^*) and predators (y^*). They also examined a spatially explicit form of the model using a cellular automaton, thereby assessing the robustness of the analytical model to the incorporation of local spatial structure. We will revisit portions of their analysis in Section 6.

3. An "Ignorant Predator" Metapopulation Model

In the model formulated by Bascompte & Solé (1998), c_y represents the per patch rate at which predators colonize a "habitable" site; i.e., a patch containing prey of type X. However, predators often must deal with imperfect information regarding their environment, which frequently can result in suboptimal movements (e.g., Zollner, 2000); i.e., movements to patches without prey of type X. The degree to which predators can track the distribution of prey is dependent upon numerous factors, including the sensory capabilities of the predator, behavioral or ecological characteristics of the prey that alter their detectability, and characteristics of the physical environment (Mason & Patrick, 1993; Brown *et al.*, 1999). In eqn (1b), predators colonize sites containing prey of type X at a rate c_y . An alternative scenario is to recognize that predators make mistakes when acting without perfect information regarding the distribution of prey. As an extreme example, suppose that predators know nothing regarding the distribution of X-type prey in the landscape. In other words, predator colonization of a patch occurs independently of whether it is occupied by an X-type prey. This produces a random-encounter

model, which we refer to as the “ignorant predator” model to highlight the fact that colonization of a site by a predator is not conditional on the occurrence of X-type prey. In the Appendix we show the equivalence of the ignorant predator model to a model formulated in terms of state transitions of patches. The ignorant predator model is as follows:

$$\frac{dx}{dt} = c_x x(1 - x - D) - e_x x(1 - y) - (e_x + \mu)xy, \quad (2a)$$

$$\frac{dy}{dt} = c_y y(1 - y - D) - e_y xy - (e_y + \psi)(1 - x)y. \quad (2b)$$

The equations for both prey and predator contain positive colonization terms. The colonization term for the prey is identical to the term in eqn (1a). However, the term in eqn (2b) reflects the probability of predator colonization of any extant patch without a predator, including patches without X-type prey (i.e., $1 - y - D$). In eqn (2a) we have decomposed the probability of extinction of prey into two terms. A fraction $x(1 - y)$ of patches are occupied only by prey, and prey on these patches have a per-patch extinction probability of e_x . The remaining patches occupied by prey also are occupied by predators. Thus, a fraction xy of patches exhibit the additive extinction probabilities intrinsic to prey and due to predation ($e_x + \mu$). To facilitate interpretation we also have decomposed the probability of extinction of predators into two terms in eqn (2b). In the fraction of patches occupied by both X-type prey and the predator (xy), predator extinction occurs with probability e_y . In patches without X-type prey, predators pay an added cost (ψ) in terms of increased probability of local extinction for mistakenly colonizing an inferior resource patch. When $\psi = 1 - e_y$, the instantaneous probability of predator extinction is 1 on a patch with no X-type prey, consistent with an extreme specialist, but differing from the model of Bascompte & Solé (1998) by allowing colonization of patches lacking X-type prey. Alterna-

tively, when $\psi = 0$, predators are functionally independent of X-type prey, consistent with a system in which predation on X-type prey occurs incidental to primary foraging pursuits of generalist predators (i.e., incidental predation, *sensu* Vickery *et al.*, 1992; Schmidt & Whelan, 1998).

In Section 6 we derive the equilibria for this ignorant-predator model, analyse the general conditions for stability, and examine the behavior of the model in response to changes in habitat destruction (D), predator colonization rate (c_y), extinction rate of prey due to predation (μ), and extinction rate of predator due to ignorance of the location of X-type prey (ψ). We also assess the robustness of the ignorant predator model to variation in local structure of the landscape by comparing results to those produced by its spatially explicit analog. First, though, we compare more closely the formulations of the ignorant predator model and the model of Bascompte & Solé (1998). We then provide the conditions necessary for equivalence of the two models.

4. Comparison of Metapopulation Models

Algebraic manipulation results in a simplified form of the ignorant predator model from eqns (2a) and (2b) as follows:

$$\frac{dx}{dt} = c_x x(1 - x - D) - e_x x - \mu xy, \quad (3a)$$

$$\frac{dy}{dt} = c_y y(1 - y - D) - e_y y - \psi y(1 - x). \quad (3b)$$

For simplicity, assume $D = 0$. Comparing eqns (1a) and (3a), the only difference in the prey equations for the two models resides in the last term. For the ignorant predator model (3a), the rate of increase of x is reduced by an amount μ in the fraction xy of patches in which both prey and predator reside. In the model of Bascompte & Solé (1998), co-occurrence of predator and prey is not explicitly addressed, because the occurrence of predators is conditional on prey. Thus, equivalence of the two prey equations is predicated on the equivalence of the last terms; namely, $\mu y \equiv \mu xy$. Likewise, equivalence of the

ignorant predator [eqn (3b)] with the omniscient predator of the Bascompte & Solé (1998) model (1b) requires that $c_y = \psi$ in eqn (3b).

5. A Spatially Explicit Predator-Prey Metapopulation Model

To determine how local colonization processes influence the dynamics of the ignorant-predator system, we developed a spatially explicit simulation model. Following Bascompte & Solé (1998), we constructed a stochastic cellular automation with four nearest neighbors coupling. We used a 100×100 lattice of patches and incorporated habitat destruction by randomly removing a specified fraction of patches from those considered to be usable, i.e., $1 - D$. After categorizing each patch as either available or destroyed, predator-prey dynamics were modeled as described below. The complete set of the state transitions is provided in Appendix A.

Initially, prey and predators were distributed randomly and independently among half of the available patches. Thus, approximately $\frac{1}{4}$ of available patches were occupied by both species at the beginning of a simulation. Extinction and colonization processes were applied stochastically on a patch-by-patch basis. The state of each available patch (empty, occupied by X-type prey, occupied by predator, occupied by both species) and its four nearest neighbors determined the particular probabilities used (Appendix A).

If a patch was occupied only by prey, extinction of prey occurred with probability e_x . However, if a patch contained both species, extinction of prey occurred with probability $e_x + \mu$ and extinction of the predator occurred with probability e_y . If no X-type prey currently occupied the patch, extinction of the predator occurred with probability $e_y + \psi$. After the state of a patch had been updated to account for extinction events, the state was saved to a new lattice for use in determining colonization.

After extinctions has been determined for the entire lattice, colonization also was modeled stochastically. If the patch was unoccupied by species i , a check was made of the state of each of its four-nearest neighboring patches. A neighbor-

ing patch occupied by species i could colonize the focal patch with probability c_i . Adopting this rule ensured that colonization was a local process. Moreover, independence of colonization probabilities among patches resulted in a functional probability of colonization that varied with the number of neighboring patches occupied by i . Specifically, the probability of colonization of a patch in the explicit model is $1 - (1 - c_i)^n$, where n is the number of neighboring patches occupied by species i , $0 \leq n \leq 4$. After the state of a patch had been updated to account for colonization events, the state was saved to the new lattice.

Our interest in simulation was to compare results of our analytical model (3), in which dispersal occurs globally, with a model in which dispersal was constrained to occur locally. Thus, we conducted simulations until a steady state was attained in the fraction of available patches occupied by prey and predator. A steady state was assumed to occur when three iterations yielded a change of ≤ 0.0001 in the running average of patch occupancy (excluding the first 20 iterations to reduce the influence of initial conditions). Because of the discrete nature of the simulations, equilibrated values conceivably could be influenced by the timing of the census of patches relative to the life cycles of the populations (e.g. Caswell, 1989). Thus, we computed equilibrated values based on the average of censuses conducted before and after colonization. Results presented below are averages of three replicate runs for each set of parameter values.

6. Results

6.1. EQUILIBRIA AND STABILITY ANALYSIS

As noted by Bascompte & Solé (1998), there are three equilibria for the model in eqn (1). The first two, $E_0 = (0, 0)$ and $E_1 = (x_1, 0)$, are boundary equilibria. Denote the critical fractions of habitat destruction at which predator and prey become extinct as D_{c_1} and D_{c_2} , respectively. E_0 is stable if $D > D_{c_2} = 1 - (e_x/c_x)$ and unstable if $D < D_{c_2}$. For E_1 , $x_1 = 1 - D - (e_x/c_x)$, and thus E_1 exists if and only if $D < D_{c_2}$. E_1 is stable if $D > D_{c_1} = 1 - e_x/c_x - e_y/c_y$ and unstable if $D < D_{c_1}$. The third equilibrium, $E^* = (x^*, y^*)$,

is an interior equilibrium with x^* and y^* given by (Bascompte & Solé, 1998)

$$x^* = \frac{1}{2c_x} \left[\Gamma + \left(\Gamma^2 + 4c_x \mu \frac{e_y}{c_y} \right)^{1/2} \right], \quad (4a)$$

$$y^* = x^* - \frac{e_y}{c_y}. \quad (4b)$$

In eqn (4a), $\Gamma = c_x(1 - D) - e_x - \mu$. Because of the conditional nature of y on x , E^* exists if and only if $D < D_c$. However, it can be shown (Appendix A) that there exist critical values D_c and μ_c such that E^* is unstable for $D < D_c$ and $\mu > \mu_c$, or for $D > D_c$ and $\mu < \mu_c$. The region of instability can be substantial for reasonable parameter values.

Four possible equilibria exist for the ignorant-predator model in eqn (2). The first two, E_0 and E_1 , are identical to those discussed previously in the model of Bascompte & Solé (1998). A third boundary equilibrium, $E_2 = (0, y_2)$, exists because predators are no longer constrained to occur only on patches containing X-type prey. Thus, at E_2 , X-type prey are extinct, but predators persist due to resource supplementation. The equilibrium fraction of patches occupied by predators in the absence of X-type prey is $y_2 = 1 - D - (e_y + \psi)/c_y$. Existence of E_1 and E_2 can be expressed in terms of critical values of habitat destruction: E_1 exists if and only if $D < D_{x_1} = 1 - (e_x/c_x)$, and E_2 exists if and only if $D < D_{y_1} = 1 - (e_y + \psi)/c_y$. A complete stability analysis of these boundary equilibria is provided in Appendix A.

The fourth equilibrium of the ignorant-predator model is given as $E_i^* = (x_i^*, y_i^*)$, where

$$x_i^* = \frac{1}{b} (c_y(c_x - \mu)(1 - D) - c_y e_x + \mu(e_y + \psi)), \quad (5a)$$

$$y_i^* = \frac{1}{b} (c_x c_y (1 - D) - c_x \psi D - c_x e_y - e_x \psi) \quad (5b)$$

and $b = c_x c_y + \mu \psi$. Conditions for the existence of E_i^* are provided in Appendix A. The Jacobian

at E_i^* is given as

$$\mathbf{J}_i^* = \begin{pmatrix} -c_x x_i^* & -\mu x_i^* \\ \psi y_i^* & -c_y y_i^* \end{pmatrix}.$$

For a 2×2 Jacobian, \mathbf{J} , stability exists if the determinant, $\text{Det}(\mathbf{J}) > 0$ and the trace, $\text{Tr}(\mathbf{J}) < 0$ (Gurney & Nisbet, 1998). For \mathbf{J}_i^* , $\text{Det}(\mathbf{J}_i^*) = (c_x c_y + \mu \psi) x_i^* y_i^* > 0$ and $\text{Tr}(\mathbf{J}_i^*) = -c_x x_i^* - c_y y_i^* < 0$. Hence, E_i^* is always stable when it exists, in contrast to the interior equilibrium from the model of Bascompte & Solé (1998).

6.2. EFFECTS OF HABITAT DESTRUCTION AND RESOURCE SUPPLEMENTATION

Increasing the level of habitat destruction always leads to a smaller fraction of patches occupied by predators at equilibrium in the ignorant-predator model (Appendix A, Figs 1 and 2). The use of alternative resources by a predator in the ignorant-predator model is capable of counteracting some of the negative effects of habitat destruction on predator persistence. Specifically, resource supplementation by predators increases the proportion of additional resource patches that they can exploit, albeit with varying degrees of efficiency, from patches occupied only by X-type prey ($x - y$) to all undestroyed patches ($1 - D - y$). For this condition to be true, we must assume that all intact patches have equal amounts of some resource(s) other than X-type prey. Thus, resource supplementation permits predators to dilute the effect of habitat destruction by potentially accessing an additional fraction $1 - D - x$ of patches. From the perspective of foraging ecology, the probability of predator survival in a patch without X-type prey is related to the relative efficiency with which alternative resources in the patch can be used by predators and is measured by $1 - e_y - \psi$. As predators become less dependent on X-type prey for their survival in a patch (lower ψ), the equilibrium proportion of patches occupied increases for a given level of habitat loss (Figs 1 and 2).

For prey, the interactive effects of habitat destruction and resource supplementation by predators are more complicated. Intuitively, we might expect that increasing the level of habitat destruction should always lead to a smaller fraction of

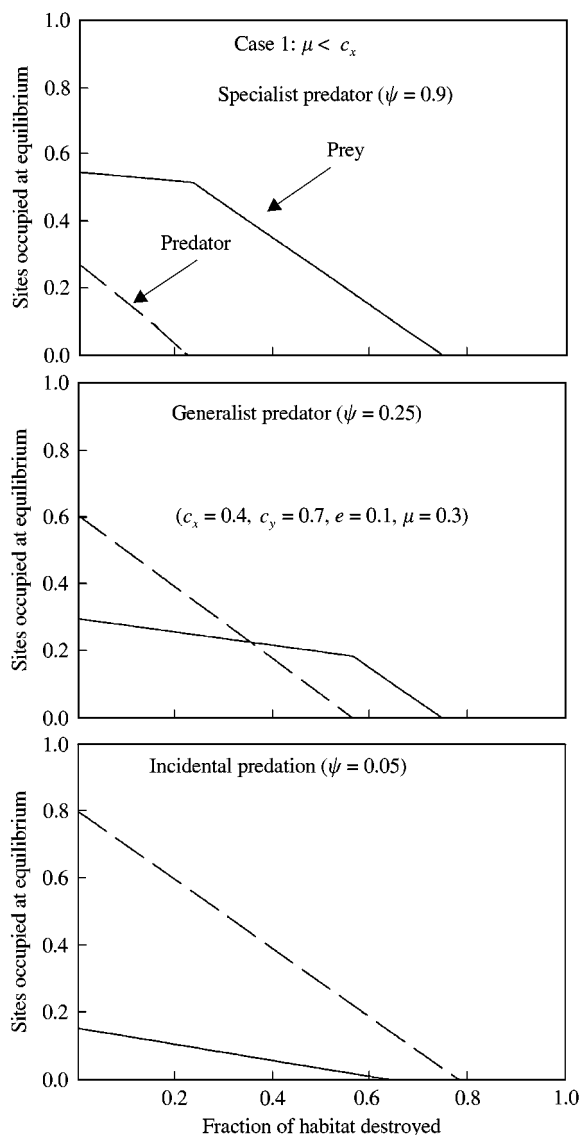


FIG. 1. The fraction of sites occupied at equilibrium for prey (solid line) and predator (dashed line) as predicted by the ignorant-predator metapopulation model (3). In this case, $\mu < c_x$. Note that prey decline monotonically as habitat destruction increases, but at a faster rate after extinction of predators. Also, note the dramatic positive impact of resource supplementation on predators, and concomitantly its negative impact on prey of type X. Resource supplementation is indexed by ψ , with lower values indicating greater levels of resource supplementation, or equivalently, less reliance on X-type prey for survival.

patches occupied by prey. However, this is not true, because under certain circumstances the effect of habitat destruction is less detrimental than the effect of predation. Specifically, the cost to prey of predation is less than the cost of habitat destruction when the probability of extinction

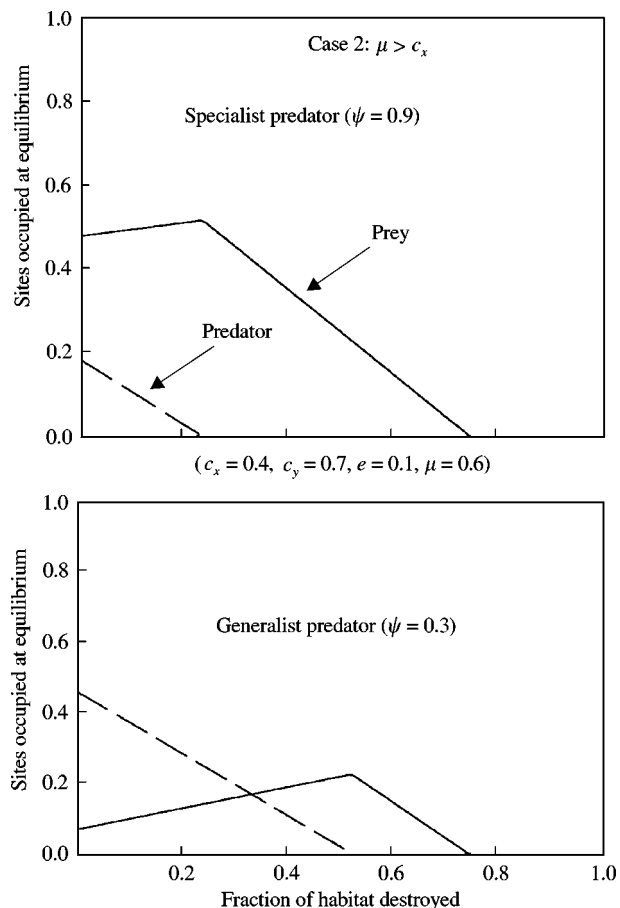


FIG. 2. A depiction comparable to Fig. 1, except in this case $\mu > c_x$. Note that the equilibrium density of prey increases as habitat destruction increases, until the point of predator extinction. The patterns with respect to resource supplementation are consistent with those from Fig. 1.

due to co-occurrence of predators and prey on a patch is less than the probability of colonization by prey of a vacant, habitable patch; i.e., $\mu < c_x$ (Appendix A). In this case the equilibrium fraction of prey patches, x^* , declines linearly with increasing habitat destruction (Fig. 1). When $\mu > c_x$ the situation is reversed and the per-patch “death” rate due to predation exceeds the per-patch “birth” rate due to colonization (Appendix A). In this case prey actually benefit from habitat destruction, because the reduction in the fraction of patches occupied by predators increases predator-free patches faster than patches are destroyed. Thus, prey “escape” from predation is facilitated by habitat loss, and x^* increases linearly with D (Fig. 2). For both cases,

when the predator suffers extinction the domain switches to E_1 , and the slope of x^* changes accordingly (Figs 1 and 2).

Resource supplementation by predators also leads to a range of predator-prey equilibrial relationships as a function of habitat destruction. The fraction of patches occupied by prey at equilibrium always exceeds the fraction occupied by specialist predators (Figs 1 and 2), consistent with the models of May (1994) and Bascompte & Solé (1998). However, for low to moderate levels of habitat destruction generalist predators can occupy a greater fraction of patches at equilibrium than X-type prey (Figs 1 and 2). And when predators are so generalized in their resource use that they need not rely on X-type prey other than incidentally, $y^* > x^*$ at all levels of habitat destruction, provided that $\mu < c_x$ (Fig. 1).

A fundamental outcome of the ignorant-predator model is that resource supplementation by predators reduces equilibrial levels of prey occupancy of patches (Figs 1 and 2). By relying on buffer prey, generalist predators are able to persist in patches without X-type prey while simultaneously using these patches as sources of colonists for patches containing X-type prey.

6.3. EFFECTS OF PREDATOR COLONIZATION RATE

Bascompte & Solé (1998) demonstrated thresholds for c_y , the per-patch colonization rate of predators. For rates below a threshold value, predators suffered extinction, whereas small increases in colonization rate above the threshold resulted in a rapid increase in the equilibrium fraction of patches occupied by predators. We analysed the ignorant-predator model (3) to determine how the equilibrium patch density of predators, y^* , was affected by c_y , and specifically to ascertain whether threshold behavior was exhibited.

Unlike the model (1) of Bascompte & Solé (1998), ignorant predators [Eqn (3)] can persist in a landscape even in the absence of X-type prey (i.e. E_2). Thus, two critical values are required to determine the range of c_y over which coexistence occurs. Let c_{y_1} and c_{y_2} be the predator colonization rates at which $x^* = 0$ and $y^* = 0$, respectively. Specifically, we can express these critical

values as

$$c_{y_1} = \frac{\mu(e_y + \psi)}{(\mu - c_x)(1 - D) + e_x}$$

and

$$c_{y_2} = \frac{c_x e_y + \psi(c_x D + e_x)}{c_x(1 - D)}.$$

Note that $c_{y_1} < 0$ when $\mu < c_x - (e_x/(1 - D))$, whereas $c_{y_1} > 0$ when $\mu > c_x - (e_x/(1 - D))$. Also note that $c_{y_2} > 0$ over the feasible range of parameter values. Consequently, when $\mu > c_x$ coexistence occurs if and only if $c_{y_2} < c_y < c_{y_1}$. Outside of this range, either predators only ($c_y > c_{y_1}$) or prey only ($c_y < c_{y_2}$) exist (Fig. 4). When $\mu < c_x$, only prey can occur for $c_y < c_{y_2}$, and coexistence occurs for $c_y > c_{y_2}$.

The equilibrium fraction of patches occupied by predators exhibits a nonlinear response to predator colonization rate, and the position and severity of the threshold varies as a function of habitat destruction and resource supplementation (Fig. 3). In general, habitat destruction increases the colonization rate necessary for predator persistence in a landscape. Specialist predators are much more severely affected by habitat loss, both in terms of the threshold level of colonization required for persistence and in terms of the equilibrium occupancy attained (Fig. 3). As the per-patch probability of prey extinction due to predation (i.e. μ) increases, the equilibrium density of predators declines because fewer patches contain X-type prey. For a given level of habitat destruction, increases in the probability of extinction of X-type prey due to predation have a greater negative impact on specialist predators (Fig. 3).

6.4. COMPARISON OF ANALYTICAL AND SIMULATION MODELS

After comparing their analytical model and cellular automata, Bascompte & Solé (1998, p. 391) concluded that the predictions made by the two approaches were similar, although "minor differences arise as a consequence of real space effects". However, inspection of a subset of their results suggests that differences can be substantial. We have illustrated their simulation

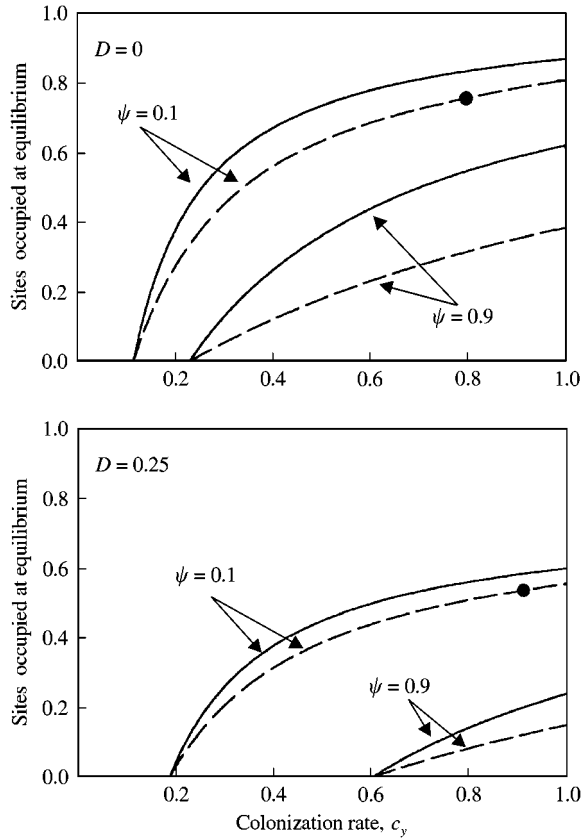


FIG. 3. The fraction of sites occupied at equilibrium by the predator as a function of its colonization rate, for the ignorant-predator model. Resource supplementation has a dramatic impact on the equilibrium density of predators, and the critical colonization rate necessary for predators to persist is related in a nonlinear fashion to D and ψ . The solid dots represent critical rates of colonization, c_{y1} , above which only predators exist. This condition only occurs when $\mu > c_x - (e_x/(1 - D))$. Parameter values are $c_x = 0.7$, $e_x = e_y = 0.1$: (—) $\mu = 0.2$; (---) $\mu = 0.8$.

results and superimposed their analytical model's corresponding predictions for a set of parameter values used in their study (Fig. 4). In an intact landscape, equilibril densities of predator and prey are considerably greater than predicted by their analytical model; the increase for predators is nearly an order of magnitude. In addition, both species persisted over the time span of the simulations (thousands of iterations in a spatially structured landscape at much greater levels of habitat destruction than predicted by their analytical model (Fig. 4). Initial comparisons of the ignorant-predator model and its spatially explicit counterpart also suggested differences. In a single-species system, such as exists after extinction

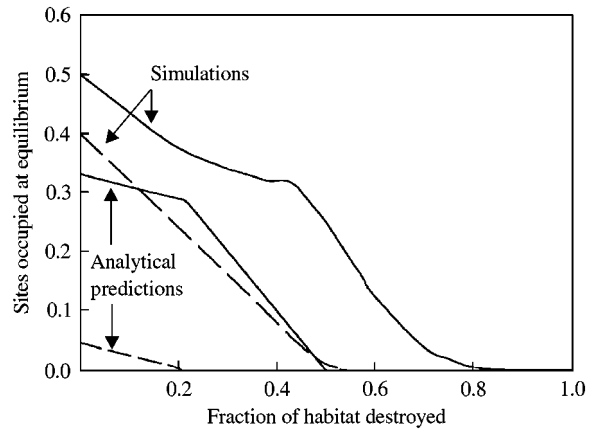


FIG. 4. A comparison of analytical predictions from the mean field model and simulation results from the spatially explicit model of Bascompte & Solé (1998). Note the large discrepancy in results for the predator equilibria from the two models. The parameter values are taken from Fig. 7 of Bascompte & Solé (1998): $\mu = 0.5$, $c_x = 0.4$, $c_y = 0.7$, $e_x = e_y = 0.2$: (—) Prey; (---) Predator.

of predators, Sato *et al.* (1994) have shown that conditions for persistence are more restrictive for a spatially explicit model than for an equivalent mean field model. We believe that much of the discrepancy between results of the spatially structured model and the mean field model, as well as the apparent contradiction with the findings of Sato *et al.* (1994), arises from differences between the nominal colonization rates, c_i , of the analytical models and the effective colonization rates, c'_i , of the spatially explicit models (see below).

Colonization rates are constants in the analytical models (1) and (2). They represent the probability of settlement of a vacant, habitable patch, and this probability is independent of the status of neighbouring patches. In contrast, effective colonization rates in the spatially explicit models are determined by both the nominal colonization rate and by the status of neighboring patches, which in turn is determined by the occupancy of species i . Thus, the effective colonization rate varies both spatially and temporally. As a first approximation, assume that the probability of occupancy of neighboring patches follows a binomial distribution. Then for the case of four nearest-neighbor patches,

$$c'_i = \sum_{n=1}^4 \binom{4}{n} k^n (1 - k)^{4-n} (1 - (1 - c_i)^n), \quad (6)$$

where k is the fraction of all possible patches occupied by species i and n is the number of neighboring patches occupied by species i . For a fixed k , an increase in the nominal rate of colonization increases the effective rate of colonization because an occupied neighboring patch is more likely to serve as a source of colonists. Likewise, for a fixed c_i , an increase in the overall density of occupied patches increases the effective rate of colonization because more neighboring patches are likely to be occupied on average. In our spatially explicit model, c represents the probability of an empty patch being colonized only if it has a single occupied neighbor. In contrast, c in the mean field model is independent of local spatial or temporal variation in patch occupancy. The difference is important, because it captures a critical biological feature of spatially explicit systems, namely, distance and density effects on colonization processes.

To compare our analytical and simulation results, we calculated effective colonization rates from eqn (6) for each steady state produced by the simulation model. These effective colonization rates were then used in eqn (5) to compute equilibrium values for predator and prey under the ignorant-predator model. If coexistence failed to occur, the appropriate boundary equilibria were used.

A substantial quantitative improvement was made when comparing simulation results to analytical predictions based on effective colonization rates (e.g. Fig. 5) as opposed to nominal colonization rates (Fig. 1). Simulation results for predators agreed reasonably well with analytical predictions, although the predictions consistently were better for generalist predators than for specialists. Predators responded to changes in resource supplementation as predicted, whereas prey did not (Figs 5 and 6). When $\mu < c_x$, predictions for prey were qualitatively comparable to simulation results (Fig. 5). However, when $\mu > c_x$, predictions and simulation results for prey matched poorly (Fig. 6). In all instances, spatial structure prolonged the coexistence of species when confronted with habitat destruction.

The disparities between results of the analytical and simulation models are attributable, at least in part, to the inclusion of spatial structure and of discrete time steps in the latter (Durrett & Levin, 1994). The spatial structure imposed by

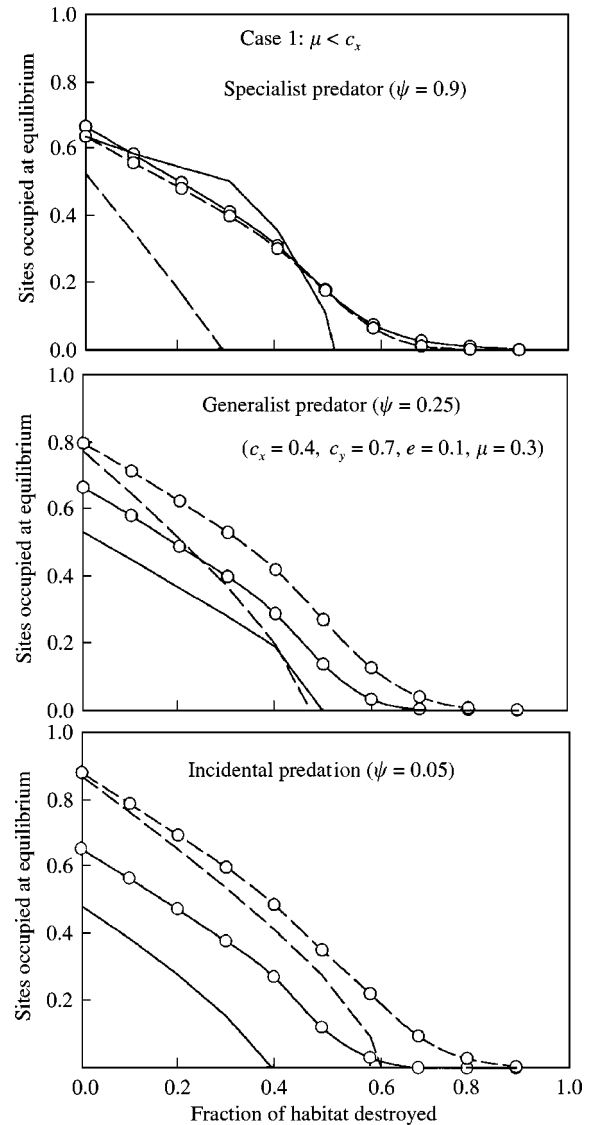


FIG. 5. A comparison of results from the ignorant-predator model (3) with its spatially explicit counterpart (circles), for the case where $\mu < c_x$. The effective colonization rate, c_i , was used to compute predicted equilibrium values for the analytical model, as described in the text. Thus, the equilibrium values for the ignorant-predator model are greater than those in Fig. 1, where the nominal colonization rates, c_i , were used. Parameter values are the same as those used in Fig. 1.

restricted dispersal leads to an occupancy pattern for neighboring patches that is more aggregated than a binomial distribution. Rather, restricting colonization to neighboring patches leads to aggregations of patches containing predators and prey (Bolker & Pacala, 1997). Our simulations begin with random spatial patterns, but local aggregations offer high probabilities of recolonization

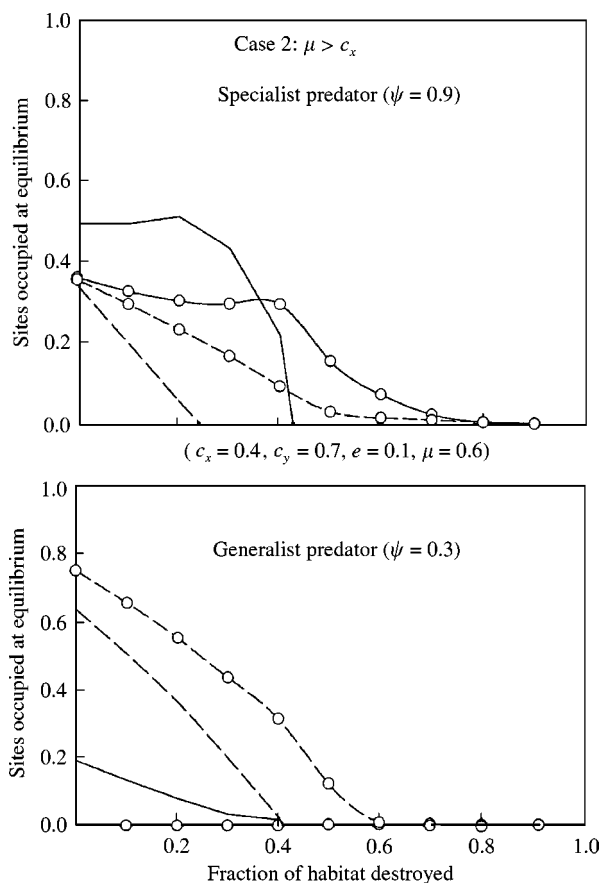


FIG. 6. A comparison of results from the ignorant-predator model (3) with its spatially explicit counterpart (circles), for the case where $\mu > c_x$. The effective colonization rate, c'_x , was used to compute predicted equilibrium values for the analytical model, as described in the text. Thus, the equilibrium values for the ignorant-predator model are greater than those in Fig. 2, where the nominal colonization rates, c_i , were used. Parameter values are the same as those used in Fig. 2.

following extinctions, and these local aggregations can be quite persistent. Declines in occupancy rate with increased destruction in the spatially explicit model are more gradual and linear than those in the analytical model, presumably due to the non-random clustering of predator and prey in the former (Figs 5 and 6).

Discrete time steps in the spatially explicit model permit prey to escape extinction even when predators are common and widespread by incorporating a time lag into the dynamics. Prey can safely colonize sites containing predators, with no ill effects incurred until the following time step. Similarly, specialist predators are allowed to invade patches without prey, even

though they become extinct in the succeeding iteration. This effect of discrete time steps, and the resulting departure from analytical predictions, becomes more pronounced as the probability of extinction increases. That is, as the expected duration of persistence decreases in the analytical model, the impact of persisting for one additional time period in the discrete version is more pronounced. Thus, the differences between our discrete and continuous time models are greater for specialist than for generalist predators. After a sufficient period of time has elapsed, the fraction of sites occupied by predator and prey attains a steady state. However, the spatial pattern of predator and prey continues to shift across the landscape. Such shifts are emergent properties of spatially structured models of interacting populations with restricted dispersal (Keitt & Johnson, 1995; Bolker & Pacala, 1999).

One important and non-intuitive consequence of spatial structure and discrete time was the promotion of coexistence of predator and prey over a wider range of habitat destruction than predicted by our analytical results (Figs 5 and 6). Similarly, spatial heterogeneity has been shown to increase coexistence of species in theoretical (Keitt, 1997) and experimental (Huffaker, 1958) food webs.

7. Summary and Discussion

The ignorant-predator model (2) extends the study of predator-prey metapopulations by incorporating resource supplementation. Equilibrium densities for coexisting species are always stable for the ignorant-predator model, whereas instability commonly occurs for the model of Bascompte & Solé (1998). The two models produced comparable results in some ways, but not in others. We highlight these comparisons below by expanding on some of the conclusions reached by Bascompte & Solé (1998):

(1) Specialist predators are driven extinct by lower values of habitat destruction than prey. However, resource supplementation counteracts this effect, and generalist predators can be less sensitive to habitat loss than the focal prey species.

(2) The equilibrium fraction of sites occupied by the predator exhibits a nonlinear response to

reductions in their colonization rate. This threshold response is more pronounced for generalist than for specialist predators. Conversely, generalist predators are more capable of persisting when their colonization rates are low.

(3) Following extinction of predators, the negative effect of additional habitat loss on regional prey abundance is intensified.

(4) Although the equilibrium fraction of sites occupied by prey is reduced due to predation, the effects of predation and habitat destruction on prey are complementary. When the risk of local extinction due to predation exceeds the rate at which patches are colonized, habitat destruction can actually increase the equilibrium fraction of sites occupied by prey.

(5) Our reanalysis suggests that substantial differences can occur between the predictions of the analytical model of Bascompte & Solé (1998) and their spatially explicit stochastic model. Much of the differences can be attributed to a constant, nominal colonization rate in the analytical model versus a distance- and density-dependent colonization rate in the spatially explicit formulation. Additional differences are due to endogenous patterns of patch occupancy and time lags in spatially explicit models.

Modeling efforts to date have focused on the effects of habitat destruction on specialist predators (May, 1994; Kareiva & Wennergren, 1995; Nee *et al.*, 1997; Bascompte & Solé, 1998). Certainly, these efforts have been justified, as the negative impacts of habitat loss on top predators are well established (see Belovsky, 1987; Hoogesteijn *et al.*, 1993; Hunter, 1996). In many landscapes, though, human degradation and alteration of native habitat have occurred for centuries. In addition, top predators may be persecuted and subjected to extirpation before habitat destruction becomes important (e.g., Palomares *et al.*, 1995). Under either of these scenarios, generalist predators are likely to proliferate at the expense of specialists. Our results suggest that in landscapes already subjected to disturbance, prey species may be more imperiled than predators. This is particularly true for prey which serve solely as an incidental source of sustenance for predators. For instance, populations of ground-nesting songbirds in grassland habitats of the central United States have

suffered from habitat loss and fragmentation (Hagan & Johnston, 1992; Johnson & Schwartz, 1993), and recent evidence suggests that generalist predators may contribute significantly to the problem (Keyser *et al.*, 1998; Gehring & Swihart, unpubl. data). Increased destruction of artificial nests of tetraonids due to generalist avian predators also has been linked to habitat fragmentation in Fennoscandia (Andrén *et al.*, 1985). Thus, our results suggest that increased attention should be focussed on the fate of prey species subjected to predation by generalist species which have adapted well to the loss or degradation of native habitat.

Our results also predict that prey colonization rate and the risk of prey extinction due to predation interact in a non-intuitive manner to affect the equilibrium densities of prey. High risk of extinction due to predation (relative to prey colonization rate) depresses the equilibrium fraction of patches occupied by both species. However, the effect of habitat destruction on equilibrium density is less severe for both species when $\mu > c_x$, and prey can even benefit under these circumstances (Fig. 2). The risk of prey extinction is influenced by the functional and numerical response of the predator at a local level. Predator responses in turn are linked to mobility (de Roos *et al.*, 1998), and presumably to determinants of niche breadth and population growth (Wolff, 1999). From the perspective of prey, colonization rate is influenced most notably by niche breadth, or the ability to use resources in the altered habitat surrounding patches (Hansson, 1991; Andrén, 1994; Wolff, 1999). Thus, future studies should explore the relation between the risk of prey extinction due to predation and the niche breadth of prey and predator.

The level of spatial detail to include in a modeling endeavor is an important consideration that can affect conclusions about the system being studied (Durrett & Levin, 1994). In our analytical formulation, a principal objective was to extend the model proposed by Bascompte & Solé (1998) to allow for resource supplementation. Thus, we used a pair of ordinary differential equations, or mean field approach, for consistency with their earlier work. We also introduced spatial structure explicitly into the system by means of our cellular automaton. Although our

main conclusions were unaffected by the level of model detail chosen, interesting differences arose in some characteristics of the system. For instance, the spatially explicit approach revealed the role of endogenous patterns of patch occupancy that cannot be shown in the mean field model. For species characterized by long-distance dispersal, such as some pelagic-spawning fishes (Moyle & Cech, 1996), the mean field model may be a more appropriate framework than a spatially structured model. However, attention to the differences between the two approaches certainly is warranted in biological systems characterized by restricted dispersal relative to the scale at which metapopulation persistence is measured. Although beyond the scope of this paper, we believe that such attention in the future could be applied toward developing fully spatial stochastic analytical models. Recently, interspecific competition models of this type have been developed by deriving equations for the dynamics of the mean densities and spatial covariances; i.e., the first two spatial moments of a system (Bolker & Pacala, 1997, 1999). In principle, spatial moment equations also could be used to characterize predator-prey systems such as the one dealt with in the current paper.

Finally, we consider the implications of our results for community structure. In landscapes subjected to habitat destruction, generalist predators are at a distinct advantage relative to specialists. This finding is consistent with empirical studies documenting the importance of buffer prey species to generalist predators during periods of scarcity of focal prey (e.g., Erlinge, 1987; Hanski & Korpimäki, 1995). Thus, habitat destruction does not necessarily result in a reduction in the length of food chains. Rather, our results imply that habitat destruction will favor a shift to predators capable of resource supplementation. Moreover, species of prey that are uncommon and minor components of the diet of generalist predators may face the greatest risk of extinction.

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APPENDIX A
Equivalent Formulation for Ignorant Predator Model

Here we demonstrate the equivalence of our formulation for the ignorant predator model with a formulation focusing on state-transitions of patches. In addition to the terminology already introduced, let u = prey-only patches, v = predator-only patches, and z = patches with both species. Then $x = u + z$, $y = v + z$, $v = (1 - x)y$ and $z = xy$. The system of ordinary differential equations for u , v , and z can be written as follows:

$$\frac{du}{dt} = c_x(u + z)[1 - u - v - z - D] - e_xu - c_yu(v + z) + e_yz.$$

The bracketed term refers to empty patches. Also, colonization of prey-only patches by predators changes the patch from state u to z (third term) and extinction of predators from z -type patches changes them to state u (fourth term). The equation for dv/dt is

$$\frac{dv}{dt} = c_y(v + z)[1 - u - v - z - D] - e_yv - \psi v - c_xv(u + z) + e_xz + \mu z.$$

The last term describes the transition of a patch with both species (z) to a patch with predators only (v) due to predation. Finally the equation for dz/dt is

$$\frac{dz}{dt} = c_yu(v + z) + c_xv(u + z) - (e_x + e_y + \mu)z.$$

The last term describes transitions out of state z due to “intrinsic” death rates and to predation. It follows from the identities above that, because $z = xy$, i.e., the fraction of patches occupied by both predator and prey,

$$\frac{dx}{dt} = \frac{du}{dt} + \frac{dz}{dt} = c_x x(1 - x - D) - e_x x - \mu xy$$

and because $v = (1 - x)y$, i.e., the fraction of patches occupied by predator only,

$$\frac{dy}{dt} = \frac{dv}{dt} + \frac{dz}{dt} = c_y y(1 - y - D) - e_y y - \psi(1 - x)y.$$

These are eqns (3a) and (3b).

Stability Analysis

We first examine the stability of E^* for the model of Bascompte & Solé (1998). The Jacobian of E^* is given by

$$\mathbf{J} = \begin{pmatrix} c_x(1 - D) - e_x - 2c_x x^* & -\mu \\ c_y y^* & -c_y y^* \end{pmatrix}.$$

Note that $\text{Det}(\mathbf{J}) = c_y y^* \sqrt{\Gamma^2 + 4c_x \mu e_y / c_y}$, which is always positive (consult the text for a definition of Γ). Hence, E^* is stable if the $\text{Tr}(\mathbf{J}) < 0$, and unstable if $\text{Tr}(\mathbf{J}) > 0$ (Gurney & Nisbet, 1998).

Define a critical value of D , D_c , such that $D_c = D_{c_1} - (e_y/c_y)$. Then $\text{Tr}(\mathbf{J}) < 0$ can be rewritten as

$$(D_c - D)\mu < \frac{(c_x(D_{c_2} - D) + e_y)(c_x(D_{c_2} - D) + c_y(D_{c_1} - D))}{2c_x + c_y}. \tag{A.1}$$

Recall that E^* exists only if $D < D_{c_i}$, $i = 1, 2$. Thus, the quantity on the right-hand side of the inequality (A.1) is positive. Now define a critical value of μ , μ_c , such that

$$\mu_c = f(D) = \frac{(c_x(D_{c_2} - D) + e_y)(c_x(D_{c_2} - D) + c_y(D_{c_1} - D))}{(D_c - D)(2c_x + c_y)}.$$

We can show that $\text{Tr}(\mathbf{J}) > 0$ for $D < D_c$ and $\mu > \mu_c$. For the parameter values used in Fig. 3 of Bascompte & Solé (1998), $D_{c_1} = 0.514$ (thus defining an upper limit for the existence of E^*), $D_c = 0.403$, and the form of μ_c is illustrated in Fig. A1 along with the regions of existence and instability of E^* in (D, μ_c) space.

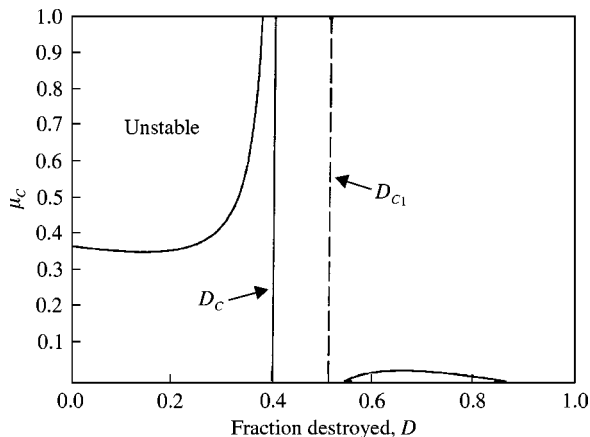


FIG. A1. Critical values of μ and D in relation to regions of instability for the interior equilibria of the model formulated by Bascompte & Solé (1998). The portion of the curve to the right of D_{c1} is plotted only for completeness, as it lies beyond the region of coexistence. Parameter values are $\mu = 0.6$, $c_x = 0.4$, $c_y = 0.9$, $e_x = 0.15$, $e_y = 0.1$.

For the ignorant-predator model, we examine the stability properties of E_1 by noting that the Jacobian at E_1 is

$$\mathbf{J}_1 = \begin{pmatrix} -c_x x_1 & -\mu x_1 \\ 0 & c_y(1-D) - e_y - \psi(D + (e_x/c_x)) \end{pmatrix}.$$

Because the eigenvalues are represented by the diagonal elements of \mathbf{J}_1 , E_1 is stable only if $c_y(1-D) - e_y - \psi(D + (e_x/c_x)) < 0$. In terms of D , E_1 is unstable if $D < D_{x_2}$, where D_{x_2} is given by

$$D_{x_2} = \frac{c_x c_y - c_x e_y - e_x \psi}{c_x(c_y + \psi)}.$$

The Jacobian at E_2 for the ignorant-predator model is

$$\mathbf{J}_2 = \begin{pmatrix} c_x(1-D) - e_x - \mu(1-D - (e_y + \psi)/c_y) & 0 \\ \psi y_2 & -c_y y_2 \end{pmatrix}.$$

In analogous fashion to E_1 , E_2 is stable only if $c_x(1-D) - e_x - \mu(1-D - (e_y + \psi)/c_y) < 0$. In terms of D , E_2 is unstable if $D < D_{y_2}$, where

$$D_{y_2} = 1 - \frac{c_y e_x - \mu(e_y + \psi)}{c_y(c_x - \mu)}.$$

E^* for the ignorant predator model exists if and only if $D < D_{x_2}$ and $D < D_{y_2}$. Conditions for the stability of E_i^* are given in the text.

Effects of Resource Supplementation and Habitat Destruction

Next, we turn our attention to the effects of ψ and D on x^* and y^* in the ignorant-predator model. Consider x^* and y^* as functions of ψ and D , denoted $F(\psi, D)$ and $G(\psi, D)$, respectively. Note that

$$\frac{\partial F}{\partial \psi}(\psi, D) = \frac{1}{(c_x c_y + \mu \psi)^2} \times \left(\mu c_x c_y D + c_y e_x + \mu^2 c_y \left(1 - D - \frac{e_y}{c_y} \right) \right) > 0$$

and

$$\frac{\partial G}{\partial \psi}(\psi, D) = \frac{-1}{(c_x c_y + \mu \psi)^2} \times \left(c_x D + e_x \right) c_x c_y + \mu c_x c_y \left(1 - D - \frac{e_y}{c_y} \right) < 0,$$

for $0 \leq D < D_{x_2}$ and $0 \leq D \leq 1$. Thus, for any fixed value of habitat destruction, x^* increases with ψ , albeit at a declining rate, whereas y^* is negatively related to ψ , with the rate of change becoming less negative as ψ increases. In a similar fashion, we can examine the influence of D on x^* and y^* by noting that

$$\frac{\partial F}{\partial D}(\psi, D) = \frac{c_y(\mu - c_x)}{c_x c_y + \mu \psi}$$

and

$$\frac{\partial G}{\partial D}(\psi, D) = -\frac{c_x(c_y + \psi)}{c_x c_y + \mu \psi}.$$

Thus, for any fixed value of ψ , x^* increases with D if $\mu > c_x$ and decreases with D if $\mu < c_x$. In contrast, y^* always decreases with increasing D .

State Transitions for the Spatially Explicit Model

Let the four states of habitable patches be represented by 0 (empty), 1 (prey only), 2 (predator only), and 3 (both species). Further, let p_{ij} represent the probability of transition from state j to state i . Finally, let n_x and n_y represent the number of neighboring patches occupied by

prey and predator, respectively ($0 \leq n_i \leq 4$). Then the following matrix of i rows and j columns represents the entire set of transition probabilities, assuming that extinction and recolonization events for a single patch do not both occur within a given time step:

$$\begin{bmatrix} (1 - c_x)^{n_x}(1 - c_y)^{n_y} & e_x(1 - c_y)^{n_y} & (e_y + \psi)(1 - c_x)^{n_x} & (e_x + \mu)(e_y + \psi) \\ (1 - (1 - c_x)^{n_x})(1 - c_y)^{n_y} & (1 - e_x)(1 - c_y)^{n_y} & (1 - (1 - c_x)^{n_x})(e_y + \psi) & (1 - e_x - \mu)e_y \\ (1 - c_x)^{n_x}(1 - (1 - c_y)^{n_y}) & e_x(1 - (1 - c_y)^{n_y}) & (1 - c_x)^{n_x}(1 - e_y - \psi) & (e_x + \mu)(1 - e_y - \psi) \\ (1 - (1 - c_x)^{n_x})(1 - (1 - c_y)^{n_y}) & (1 - e_x)(1 - (1 - c_y)^{n_y}) & (1 - (1 - c_x)^{n_x})(1 - e_y - \psi) & (1 - e_x - \mu_x)(1 - e_y) \end{bmatrix}.$$