

REPORT

Food web structure and habitat loss

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Abstract

In this paper we explore simple food web models to study how metacommunity structure affects species response to habitat loss. We find that patch abundances and extinction thresholds vary according to the kind of food web. Second, for intermediate species, a slight decrease in the exploration cost of the better competitor has a strong effect on the extinction threshold of the poorer competitor. When predicting extinction risk one should consider not only the amount of habitat destroyed, but also the structure of the food web in which species are embedded. Both direct and indirect interactions are critical for predicting the consequences of habitat destruction.

Keywords

Metacommunity, habitat destruction, omnivory, apparent competition, intraguild predation, indirect interactions.

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INTRODUCTION

Ongoing habitat destruction is the primary cause of biodiversity loss (Pimm & Raven 2000). Little is still known about how biodiversity is reduced in complex ecological webs. The goal of this paper is to explore how metacommunity structure affects the response of food webs to habitat loss.

Previous theoretical studies of habitat loss have investigated single-species (Lande 1987; Bascompte & Solé 1996), two-species (Nee & May 1992; May 1994; Holt 1997; Nee *et al.* 1997; Bascompte & Solé 1998a,b; Namba *et al.* 1999; Swihart *et al.* 2001) and *n*-competing species models (Hastings 1980; Tilman 1994; Tilman *et al.* 1994; Kareiva & Wennergren 1995). These studies emphasize two important findings. First, the existence of a correlation between trophic rank and extinction threshold, whereby specialist predators are driven extinct before their prey (Kareiva 1987; Kruess & Tschardtke 1994; Bascompte & Solé 1998a; Gilbert *et al.* 1998; Holt *et al.* 1999; Steffan-Dewenter & Tschardtke 2000). This is in agreement with empirical observations in host-parasitoid (Kruess & Tschardtke 1994) and butterfly–plant communities (Steffan-Dewenter & Tschardtke 2000). Consequently, prey species outbreaks may be more common once their natural enemies have been driven extinct by destruction of habitat (Kruess & Tschardtke 1994). Second, habitat loss has a more severe effect on species that are better competitors but poorer dispersers (Hanski 1983; Nee & May 1992). Thus, the species most prone to extinction are the highly successful

competitor species which we might never guess are at risk (Tilman *et al.* 1994; Kareiva & Wennergren 1995).

Few studies have considered the effects of habitat loss in food webs with more than two trophic levels (but see Holt 1993 and Holt 1997 for a related study of metacommunity dynamics of food webs in heterogeneous landscapes). However, habitat destruction may yield qualitatively new consequences when considering species that are embedded in an intricate web of ecological relationships (Nee *et al.* 1997). A few empirical and experimental papers seem to confirm the context-dependence of the response of food webs to perturbations. Patterson (1984) pointed out that for small mammals in boreal forest fragments, the proportion of predators declined with habitat loss, but the proportion of insectivores remained constant and the proportion of herbivores increased. Similarly, Fox & Olsen (2000) studied the propagation of indirect effects through food webs having different degrees of complexity. They found that in reticular webs the top predator exhibited more sensitivity to perturbations on basal species than in simpler linear webs. This occurs because indirect effects (*i.e.* competition between both prey species; Wootton 1994) become increasingly important in complex, reticulate food webs (Fox & Olsen 2000).

Omnivory, defined broadly as feeding on more than one trophic level, occupies a prominent position in discussions about food web structure and dynamics. According to classical results from food web theory, omnivory destabilizes ecological communities (Pimm & Lawton 1978), whereas more recent conceptual syntheses

suggest that it should be a strongly stabilizing factor in food webs (Polis & Strong 1996; Fagan 1997; McCann & Hastings 1997; Holyoak & Sachdev 1998; McCann *et al.* 1998). This paper complements this perspective by investigating spatial persistence after human-induced habitat loss.

INTEGRATING METAPOPOPULATION MODELS

Through this paper we will integrate several basic models derived as extensions of the metapopulation model by Levins (1969). The Levins' model, which has become the centrepiece of the metapopulation paradigm in conservation biology (Hanski 1998), can be written as:

$$\frac{dR}{dt} = cR(1 - R) - eR, \quad (1)$$

where R is the proportion of patches occupied, c is the colonization rate, and e is the local extinction rate. The rate of newly colonized sites is given by the product of propagule production by the occupied sites, cR , and the proportion of sites that are not yet occupied, $1 - R$. Similarly, the rate at which occupied sites become vacant is given by the product of the extinction rate e , and the proportion of occupied sites R . This equation has a globally stable non-trivial equilibrium, given by $R^* = 1 - e/c$.

Building on the Levins' framework, Lande (1987) allowed only a fraction b of the habitat (i.e. territories) to be available. His results emphasize that we do not have to destroy all patches to extinguish a metapopulation that persists by virtue of a balance between local extinctions and recolonizations in a mosaic environment. Similarly, habitat destruction (Tilman 1994; Tilman *et al.* 1994; Kareiva & Wennergren 1995) has been represented as $d = 1 - b$ in a model derived from Eq. (1).

But how do interactions among species change patch abundances and extinction thresholds? Nee & May (1992) and Tilman *et al.* (1994) expanded the Levins' metapopulation model to two and n -competing species assuming a trade-off between competition and colonization (Tilman 1994; Tilman *et al.* 1994). Hence, Tilman (1994) considers two competing species whose interactions are structured to give a competitive hierarchy. This leads to the following equations:

$$\frac{dR_1}{dt} = c_1R_1(1 - R_1) - e_1R_1, \quad (2)$$

$$\frac{dR_2}{dt} = c_2R_2(1 - R_1 - R_2) - e_2R_2 - c_1R_1R_2 \quad (3)$$

The superior competitor, R_1 , is described by the same equation as would a species living by itself (identical to Levins' metapopulation model in Eq. (1)), and thus it is totally unaffected by the inferior competitor. The superior

competitor always displaces the inferior competitor when both species co-occur in a site, but the inferior competitor can neither invade nor displace the superior competitor from a site. The inferior competitor, R_2 , can colonize only sites in which both it and species R_1 are absent (the term $(1 - R_1 - R_2)$ in Eq. (3)). This represents interference or direct competition between both competitors. Furthermore, species R_1 can invade and displace species R_2 (the term $-c_1R_1R_2$ in Eq. (3)). A fraction d of patches destroyed can be incorporated as $(1 - R_1 - d)$ in Eq. (2) and $(1 - R_1 - R_2 - d)$ in Eq. (3). Tilman assumed a trade-off between colonization and competition and showed that habitat loss induces the selective extinction of the best competitors (Tilman *et al.* 1994). Habitat destruction lowers effective colonization rates of all species, but most has the greatest impact on species with lower colonization rates, the better competitors in Tilman's model.

The third model considered here is a specialist predator-prey metapopulation model (May 1994; Bascompte & Solé 1998a). The model can be expressed as follows:

$$\frac{dR}{dt} = c_1R(1 - R) - e_1R - \mu C, \quad (4)$$

$$\frac{dC}{dt} = e_2C(R - C) - e_2C \quad (5)$$

where R is the patch occupancy of a resource or prey, and C is the patch occupancy of a consumer or predator. This model assumes that predators need prey in order to survive in a patch, that is, C is a subset of R (this is the reason for the term $R - C$ in Eq. (5)). This model further incorporates the effect of varying levels of predator control on prey populations via the parameter μ . In this model, specialist predators are driven extinct by habitat loss before their prey (Bascompte & Solé 1998a).

Finally, we introduce Swihart *et al.*'s (2001) model (an expansion of Bascompte & Solé's 1998a model) constructed to understand the effect of habitat destruction on a generalist predator. The novelty is that the predator colonization of a patch occurs independently of patch occupation by the preferred prey. Therefore, in patches without prey, predators pay an added cost (ψ) in terms of an increase in the rate of local extinction for mistakenly colonizing an inferior resource patch. The model is written as:

$$\frac{dR}{dt} = c_1R(1 - R) - e_1R - \mu RC, \quad (6)$$

$$\frac{dC}{dt} = e_2C(1 - C) - e_2C - \psi C(1 - R) \quad (7)$$

In contrast to specialist predators, Swihart *et al.* (2001) found that habitat destruction is not as detrimental for generalist predators. Thus, habitat loss does not necessarily reduce the length of food chains as showed for specialist predators (Bascompte & Solé 1998a).

In summary, much of the theory about how habitat loss affects the dynamics of multi-species interactions deals only with simple two-species interactions or n competing species. The question that we address in the remainder of this paper is “how do these results change when we consider increasing food web complexity and indirect effects?”

METACOMMUNITY MODELS

Over the past decade, the view that food webs are highly interconnected assemblages characterized by recurrent structures has overcome the former concept of ecosystems as linear food chains. Because combinations of competition and predation can represent these common food web structures, the use of simple food web modules has been advocated to explore the repercussions of these ubiquitous interactions (McCann 2000, and references therein). We synthesize trophic and competitive interactions using models assuming that all the species have a similar population structure and habitat requirements; they are influenced by habitat loss in exactly the same way. We consider four types of food web illustrated in Fig. 1: a simple food chain, an omnivorous food web (e.g. Fagan 1997), a food web with apparent competition (e.g. Holt & Lawton 1994; Bonsall & Hassell 1997), and finally a food web with intraguild predation (e.g. Polis & Holt 1992). The model for the simple food chain (Fig. 1) can be described as:

$$\frac{dR}{dt} = c_1R(1 - R - d) - e_1R - \mu_1RC, \quad (8)$$

$$\frac{dC}{dt} = e_2C(1 - C - d) - e_2C - \psi_1C(1 - R) - \mu_2CP, \quad (9)$$

$$\frac{dP}{dt} = e_3P(1 - P - d) - e_3P - \psi_2P(1 - C). \quad (10)$$

Here R is the basal species patch density, C is the patch density of the intermediate species, and P is the patch

density of the top species. d is the fraction of sites destroyed. c_i and e_i represent colonization and extinction rates of species i . As noted above, we assume that colonization of a patch by the predator occurs independently of patch occupancy by its main prey. Therefore, in patches without prey, intermediate and top species pay an added cost (ψ_1 and ψ_2 in Eqs (9) and (10)) in terms of an increase in the rate of local extinction for mistakenly colonizing an inferior resource patch. That is, extreme specialist predators go immediately extinct in patches without their prey. When C and P are extreme generalists, ψ_1 and ψ_2 are equal to 0 (Swihart *et al.* 2001). Finally, μ_i represents the increase in mortality due to predation. Our model extends the basic ignorant predator model by Swihart *et al.* (2001) by adding an additional trophic level, with new direct and indirect interactions.

In the omnivorous food web (Fig. 1), vertical complexity is now increased relative to the simple food chain, via feeding links between the top species and the two lower trophic levels. The model can be written as:

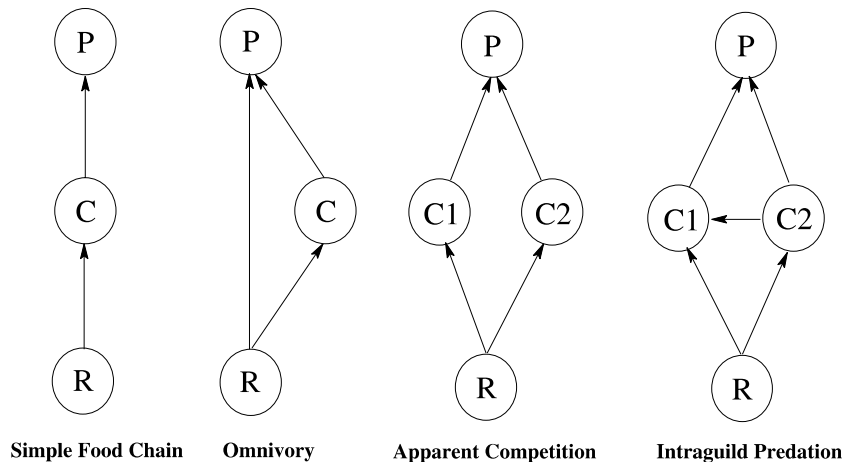
$$\frac{dR}{dt} = c_1R(1 - R - d) - e_1R - \mu_1RC - \mu_2RP, \quad (11)$$

$$\frac{dC}{dt} = e_2C(1 - C - d) - e_2C - \psi_1C(1 - R) - \mu_3CP, \quad (12)$$

$$\frac{dP}{dt} = e_3P(1 - P - d) - e_3P - \frac{\psi_2}{2}P(1 - R) - \frac{\psi_3}{2}P(1 - C), \quad (13)$$

where all parameters are defined as above (Eqs (8)–(10)). We consider omnivory in a restrictive sense, that is, top species’ persistence is maximum when both prey species are present in the same patch. We assume that an omnivorous top species needs species from two trophic levels in each patch to minimize the foraging cost (Ball 1994; Sih

Figure 1 The four types of food-web studied are, from left to right, a simple food chain, a food web including omnivory, a food web with the top species feeding on two intermediate consumers (apparent competition), and a food web with consumer 1, C_1 , feeding on the basal species and on the second consumer C_2 (intraguild predation). R denotes the basal species; C_1 and C_2 denote intermediate species; P denotes the top species. Note that in this paper we introduce a spatial component, and the food web may be incomplete in some patches.



& Christensen 2001). Thus, if ψ_2 is the cost for a top predator in a simple food web, then the cost associated in the omnivorous food web when one of the prey species is absent would be $\psi_2/2$ or $\psi_3/2$ (Eq. (13)). As a result, when omnivorous top species colonize a new patch and none of the prey species are present, the total cost, ψ_t , is:

$$\psi_t = \frac{\psi_2}{2} + \frac{\psi_3}{2}, \quad (14)$$

and the extinction rate in such an empty patch is $e_3 + \psi_2/2 + \psi_3/2$. In a similar way, when only one of the two prey species (i.e. basal or intermediate) is absent in a patch, the extinction rate is $e_3 + \psi_i/2$.

The extinction term for the top species when there is apparent competition (Fig. 1) or intraguild predation (Fig. 1) is defined similarly to that for the omnivorous top species. We assume that the top species needs the two prey species in each patch to minimize the foraging cost. In both cases, the top species feeds on two intermediate species, C_1 and C_2 . Thus, species C_1 and C_2 are engaged in apparent competition by sharing the same predator (see Fig. 1). They are also engaged in indirect competition because they share the same resource (the basal species). We assume a trade-off between competition and colonization: C_1 is a better competitor but C_2 is a better disperser. The asymmetry in colonization rates allows the coexistence of C_1 and C_2 . C_2 can not occupy patches already occupied by C_1 (this is described by the term $1 - C_1 - C_2 - d$ in Eqs (17) and (21)), and C_1 can occupy either empty patches or patches occupied by C_2 . Here, we do not assume that C_1 displaces species C_2 from patches occupied by both C_1 and C_2 as assumed by Tilman (1994). These are a less severe assumptions than that made for a purely competitive system (e.g. Tilman 1994; see Eq. (3)), and represents a less intensive competition between C_1 and C_2 . This can be translated into the following model (Fig. 1):

$$\frac{dR}{dt} = c_1 R(1 - R - d) - e_1 R - \mu_1 R C_1 - \mu_2 R C_2, \quad (15)$$

$$\frac{dC_1}{dt} = c_2 C_1(1 - C_1 - d) - e_2 C_1 - \psi_1 C_1(1 - R) - \mu_3 C_1 P, \quad (16)$$

$$\begin{aligned} \frac{dC_2}{dt} = & c_3 C_2(1 - C_1 - C_2 - d) - e_3 C_2 \\ & - \psi_2 C_2(1 - R) - \mu_4 C_2 P, \end{aligned} \quad (17)$$

$$\frac{dP}{dt} = c_4 P(1 - P - d) - e_4 P - \frac{\psi_3}{2} P(1 - C_1) - \frac{\psi_4}{2} P(1 - C_2). \quad (18)$$

Finally, when allowing C_1 to also feed on C_2 (with a similar extinction term as for the top species), we can write the following model for the food web with intraguild predation (Fig. 1):

$$\frac{dR}{dt} = c_1 R(1 - R - d) - e_1 R - \mu_1 R C_1 - \mu_2 R C_2, \quad (19)$$

$$\begin{aligned} \frac{dC_1}{dt} = & c_2 C_1(1 - C_1 - d) - e_2 C_1 - \frac{\psi_1}{2} C_1(1 - R) \\ & - \frac{\psi_2}{2} C_1(1 - C_2) - \mu_3 C_1 P, \end{aligned} \quad (20)$$

$$\begin{aligned} \frac{dC_2}{dt} = & c_3 C_2(1 - C_1 - C_2 - d) - e_3 C_2 - \psi_3 C_2(1 - R) \\ & - \mu_4 C_2 P - \mu_5 C_2 C_1, \end{aligned} \quad (21)$$

$$\frac{dP}{dt} = c_4 P(1 - P - d) - e_4 P - \frac{\psi_4}{2} P(1 - C_1) - \frac{\psi_5}{2} P(1 - C_2). \quad (22)$$

We will focus on the extinction thresholds, that is, the critical values of habitat destruction, d_c , at which a given species goes extinct. The inverse of such an extinction threshold could be considered as a measure of vulnerability to extinction due to habitat loss. In addition to the extinction threshold, the dependence of patch occupancy on habitat destruction is also important to understand the effects of habitat loss on metacommunity persistence, and we will also consider this as a benchmark for comparison. As we will show, both extinction thresholds and the decline of patch occupancy can be difficult to predict when indirect interactions are at work.

RESULTS

Our goal is to consider how food web structure alters the top species' (P) response to habitat loss for two different ecological scenarios, namely donor control and top-down control. To explore this question we analyse the metacommunity models developed in the previous section. Through this paper we explore a broad range of biologically realistic parameter combinations. The results presented here are qualitatively robust for all parameter combinations examined. Specifically, we have used numerical methods to derive the non-trivial solutions for symmetrical parameter combinations, that is, all species have the same parameter values, ranging from donor control $\mu_i = 0$ to top-down control $\mu_i = 0.7$; colonization/extinction from $c_i = 0.4$, $e_i = 0.1$ to $c_i = 0.7$, $e_i = 0.3$; and exploration cost from $\psi_i = 0.3$ to $\psi_i = 0.7$. This range of parameter combinations meets our criteria of (i) biological realism, and (ii) existence of stable non-trivial solutions.

To begin with, let us start with a donor control scenario (i.e. prey dynamics constrain the distribution of the predator, without reciprocal effects by the predator on its prey, $\mu_i = 0$). We consider intermediate (C_1 and C_2) and top (P) species as specialists, but not extreme specialists, that is, they have a high degree of selective searching behaviour.

They have an increased rate of local extinction for mistakenly colonizing an inferior resource patch ($\psi_i > 0$). We start with symmetric demographic rates, in which basal, intermediate and top species have the same colonization/extinction rates. Note that the top species' persistence is maximum when both prey species are present in the same patch. We also explored a less restrictive assumption and qualitative results remained.

For the above parameter values, a positive numerical equilibrium exists. We plot this equilibrium patch occupancy as a function of habitat destruction in Fig. 2(a). We find that:

- 1 The extinction threshold for the top species in an omnivorous web occurs at a higher level of habitat destruction ($d_c = 0.32$) than for webs with apparent competition ($d_c = 0.26$) and simple linear chains ($d_c = 0.26$). The top species goes extinct sooner in webs with intraguild predation ($d_c = 0.19$).
- 2 The top species decreases linearly but with different slopes for each type of food web. The steepest decline is for the simple and apparent competition food web, followed by the omnivory food web. The decline is less steep for intraguild predation.

Let us now consider an example of top-down control. We find that the pattern is qualitatively similar to donor control.

All else being equal, patch abundances are lower for top-down control, and the top species' extinction threshold occurs at a lower fraction of sites destroyed (compare Figs 2a and b).

Until now, we have only considered the response of the top species. What happens with the rest of the community? We plot the decline in the number of species for each food web as more habitat is destroyed in Fig. 3. Each step corresponds to the extinction of one of the species. The first species going extinct is the top species (P), and the last is the basal species (R). We find that the basal species has a similar response in each configuration (that is, its extinction threshold is the same for each configuration). This is not a surprise because after the rest of species have gone extinct, we have the same single Levins' species model. For the intermediate species (C_1 and C_2), the extinction threshold is the same for both the simple (Fig. 3a) and the omnivorous (Fig. 3b) food web. On the other hand, the extinction thresholds for the intermediate species depend on whether they are embedded in the web with apparent competition or intraguild predation. With apparent competition, C_1 and C_2 have similar extinction thresholds (Fig. 3c), whereas C_1 goes extinct before C_2 for intraguild predation (Fig. 3d). Top-down control exacerbates these differences. In general, all species go extinct sooner when control is top-down as opposed to donor (see Fig. 3).

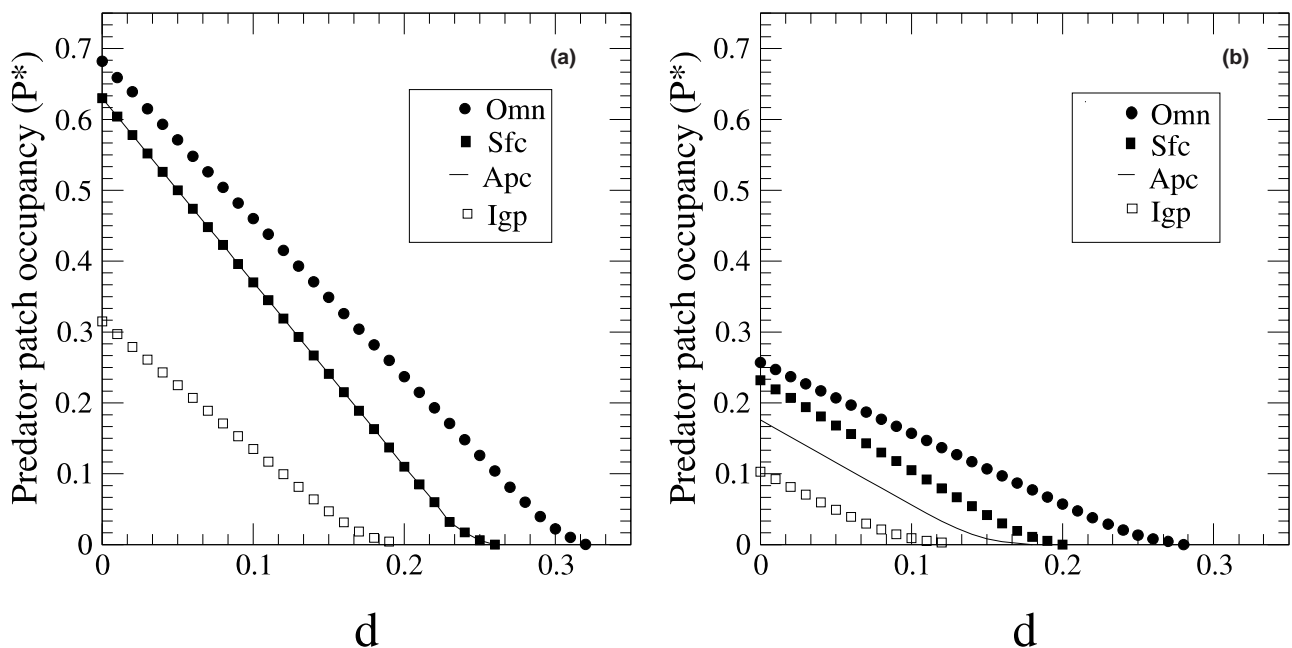


Figure 2 The patch occupancy of the top species (P) is plotted as a function of the fraction of habitat destroyed (d). As we explicitly point out in the figure, the different lines represent an omnivorous food web (●), a simple food chain (■), a food web with apparent competition (—), and a food web with intraguild predation (□). (a) represents donor control ($\mu_i = 0$), and (b) represents top-down control ($\mu_i = 0.7$). A high exploration cost or selective searching behaviour ($\psi_i = 0.6$) is assumed. Other parameters are: $c_i = 0.7$ and $e_i = 0.1$.

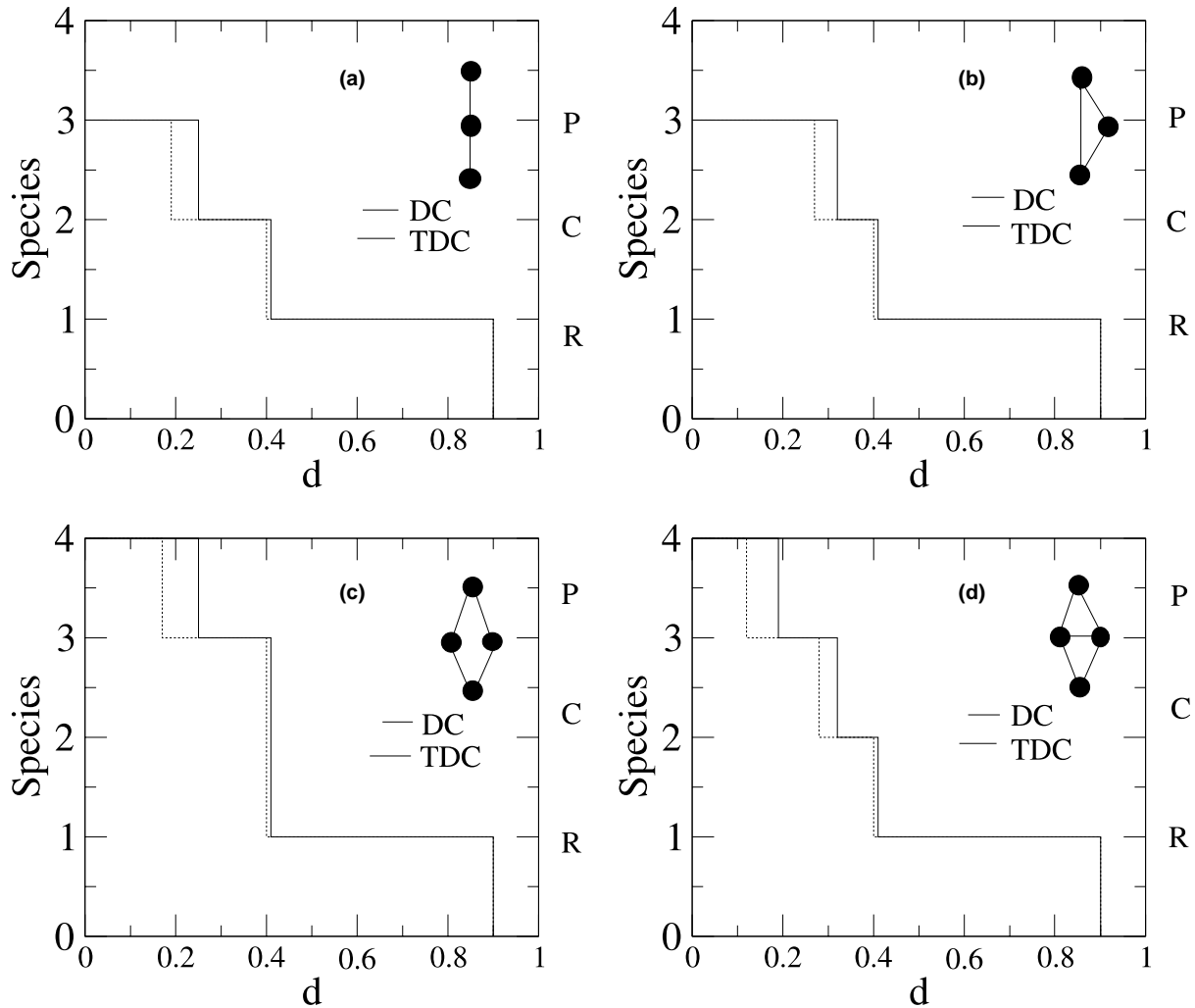


Figure 3 The fraction of extant species relative to the initial number of species is plotted as a function of the fraction of habitat destroyed. Continuous line represents donor control ($\mu_i = 0$), and dotted line represents top-down control ($\mu_i = 0.7$). The simple food chain (a) and the omnivorous web (b) have three species, whereas the food web with apparent competition (c) and intraguild predation (d), have four species. This explains the difference in the y -axis scale. Parameter values are similar to those in Fig. 2(a) (for donor control) and 2(b) (for top-down control). Each step represents the extinction of one species. From left to right, the order of extinction is for the top species (P), the intermediate species (C) and the basal species (R).

Finally, we may ask how indirect effects and non-linearities in the interactions affect the predictability of metapopulation responses to habitat loss. We explore this response in (i) an intraguild predation web, and (ii) an apparent competition web where intermediate species (C_1 and C_2) engage in direct competition. We study asymmetric demographic and exploration cost rates. Again, we have studied a broad range of biologically realistic parameter values corresponding to stable non-trivial solutions. Specifically, the range of parameter values explored here is as follows: $\mu_i = 0$ (donor control) to $\mu_i = 0.7$ (top-down control); $c_i = 0.4$, $e_i = 0.1$ to $c_i = 0.7$, $e_i = 0.3$; $c_2 = 0.3$ to $c_2 = 0.5$; $\psi_i = 0.4$ to $\psi_i = 0.7$ with ψ_1 (i.e. the exploration cost of the better competitor) from

$\psi_1 = 0$ to $\psi_1 = 1$. Our results are robust for this entire suite of asymmetric parameter combinations.

For the case of apparent competition, we observe in Fig. 4(a) that the better competitor (C_1 , dotted line) has a higher patch occupancy and a lower extinction threshold than the better colonizer, poorer competitor (C_2 , continuous line). We observe in Fig. 4(b) that a small reduction in the exploration cost of the better competitor C_1 (from $\psi_1 = 0.3$ to $\psi_1 = 0.1$) has a non-linear indirect effect on the extinction threshold of the less abundant, poorer competitor species (C_2).

Figure 5(a) shows the extinction threshold of both the better (C_1) and poorer (C_2) competitors for different values

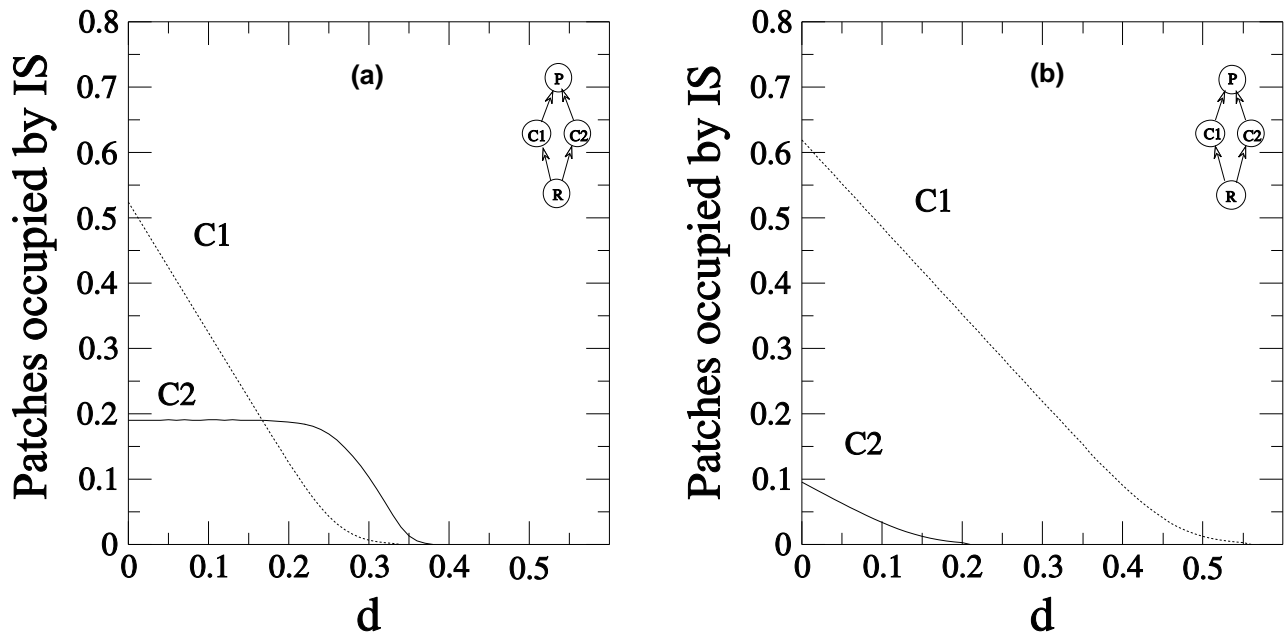


Figure 4 The patch occupancy of the two competing species (C_1 and C_2) in the food web with apparent competition are plotted as a function of the fraction of habitat destroyed (d). Continuous and discontinuous lines represent intermediate species (IS), that is, the poorer (C_2) and the better competitor (C_1), respectively. The colonization rate of the better competitor is $e_2 = 0.3$ in both cases. The other parameter values are $\mu_i = 0$, $e_i = 0.1$, $c_i = 0.7$ and $\psi_i = 0.7$. As noted, a slight decrease in the exploration cost of C_1 implies a big change in the extinction threshold for both competing species.

of the exploration cost for the better competitor. Figure 5(b) shows how the extinction threshold for the poorer competitor depends on the colonization rates of the better competitor. Evolutionary changes in the demographic parameters of one species can cascade through the food web with unanticipated consequences for the other species.

SUMMARY AND DISCUSSION

The following remarks emphasize some of our conclusions:

- 1 Food web structure alters the top species response to habitat loss.
- 2 Direct and indirect interactions between two intermediate prey decrease the patch occupancy of top predators.
- 3 Omnivory confers higher persistence for the top species for a specific value of habitat loss.
- 4 The extinction threshold of the top species is lower for top-down control than for donor control, but the difference attenuates with decreasing trophic level.
- 5 Although the top species' regional abundance is lower for top-down control, its rate of decrease as habitat is destroyed is also lower. That is, all else being equal, donor control would lead to situations with high abundance but low resistance to habitat destruction, whereas the opposite would happen for top-down control.

6 In apparent competition and intraguild predation with direct and indirect competition between intermediate species, a slight decrease in the exploration cost of the better competitor (C_1) results in a strong effect on the extinction threshold of the poorer competitor (C_2).

The present results confirm the finding that predators with high selective searching behaviour are driven extinct for lower destruction values than their prey; however, many natural communities are dominated by non-specialized consumers (Polis & Strong 1996). In the latter scenario, habitat destruction will favour generalist predators with low exploration cost (Mikkelsen 1993; Swihart *et al.* 2001). In both cases, patch abundance and extinction thresholds depend on the food web structure in which the top species are embedded.

Trophic generalization can lead to a wide range of indirect interactions in food webs such as exploitative competition, apparent competition and intraguild predation (Holt *et al.* 1999). Additionally, there is a surprising number of cases in which the removal of a predator leads to a decrease in the abundance of the focal prey (Sih *et al.* 1985). Many of these cases seem to involve indirect interactions in multispecies assemblages (e.g. competitive interactions among prey held in check by a generalist predator, Holt 1997). In this paper we have first explored the relative effect

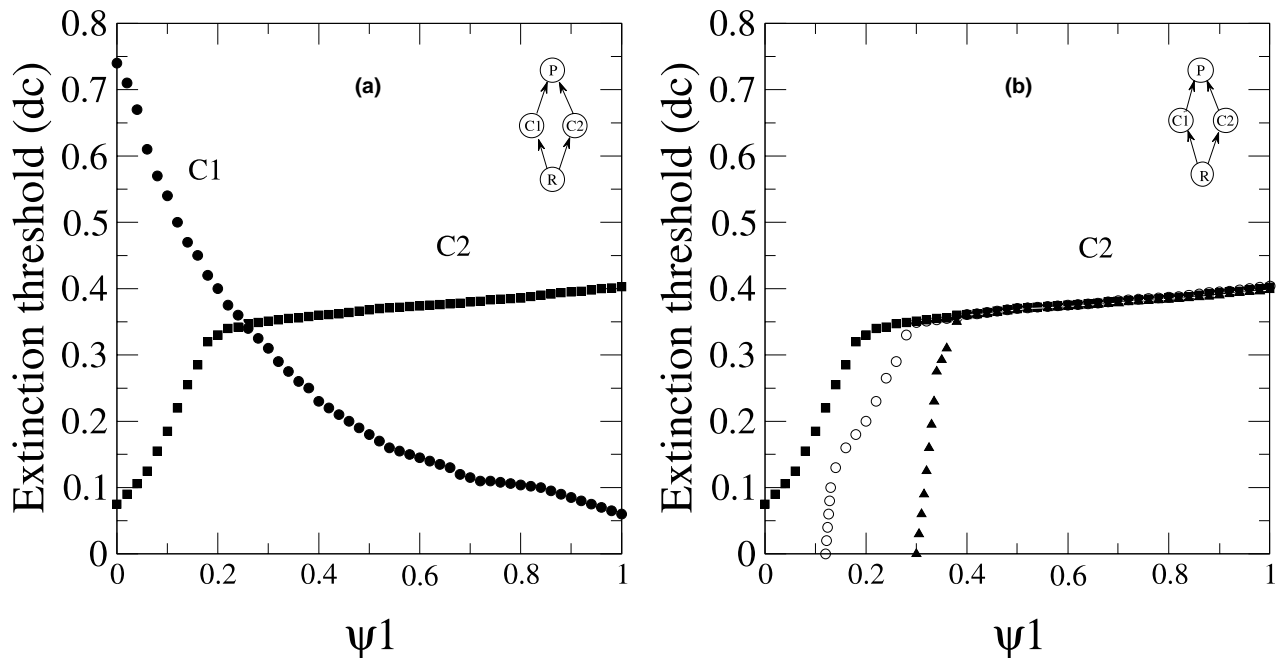


Figure 5 (a) The extinction thresholds for both competitors (C_1 and C_2) in the food web with apparent competition are plotted as a function of the exploration cost of the better competitor (ψ_1). ● corresponds to C_1 and ■ corresponds to C_2 . Parameter values are as in Fig. 4. (b) Represents the extinction thresholds for C_2 as a function of the exploration cost of the better competitor for three colonization rates of the better competitor (C_1). Colonization rates of C_1 are plotted as $\epsilon_2 = 0.3$ (■), $\epsilon_2 = 0.4$ (○) and $\epsilon_2 = 0.5$ (▲). Other parameter values are as in Fig. 4. As noted, there is a strong interaction between the exploration cost of the better competitor and the extinction threshold of the poorer competitor. Similar results remain for intraguild predation and top down-control for all the range of parameter values explored.

of direct and indirect interactions (Stone & Roberts 1991) in the context of habitat loss.

We have shown that indirect interactions from apparent competition and intraguild predation depress the extinction threshold for the top species. That is, direct and indirect interactions reduce the fraction of habitat destroyed at which the top species is driven extinct. This has been demonstrated empirically by Fox & Olsen (2000). By using microcosms, these authors showed that perturbations had a larger impact on predators embedded in reticulated food webs.

Our results add a complementary perspective to the empirical evidence pointing towards higher stability for multichannel omnivory food webs (Polis & Strong 1996; Fagan 1997; Holyoak & Sachdev 1998; McCann *et al.* 1998). In this paper, we provide evidence showing how top species may persist at higher values of habitat destruction when embedded in a food web with high levels of omnivory.

Fagan (1997) observed that the return to equilibrium after a range of disturbances in a multipatch scale was faster in omnivorous structures, although there is still a lack of theoretical interpretation (Fagan 1997). The present paper represents a first step in this direction. Note that we use stability in the sense of spatial persistence in response to

habitat loss, rather than return to the equilibrium after a local perturbation such as a reduction in abundance (Pimm & Lawton 1978; Fagan 1997).

The extinction threshold is lower for the better competitor (C_1) than for the poorer competitor (C_2) for a broad range of parameter values. This result is in agreement with previous results from single trophic-level models (Tilman 1994; Tilman *et al.* 1994, 1997), according to which the initially most abundant species in undisturbed habitat fragments can be the most susceptible to eventual extinction. However, as shown in this paper, the order of extinction can change dramatically depending on the exploration cost of the best competitor.

Species are typically enmeshed in an entangled web of direct and indirect interactions. Our results suggest that the response of the metacommunity to disturbances can be a complex interaction of different trends. These results call for extreme caution when the goal is the management of endangered species in fragmented habitats. Also, minor changes in the exploration cost of better competitors can have a large influence on the regional abundance of poorer competitors. This emphasizes how evolutionary changes at the level of generalization of one species may cascade through the rest of the community (Schmitz 1998).

In summary, patch abundances and extinction thresholds are not only determined by demographic rates (Levins 1969), behavioural and life history traits (Lande 1987), competitive-colonization abilities (Tilman 1994) and landscape properties (Bascompte & Solé 1996), but also by the structure of the food web in which the species are embedded.

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