

Ecological network meltdown from habitat loss and fragmentation

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1 THRESHOLDS IN HABITAT FRAGMENTATION

Current rates of habitat destruction are extremely high. Habitat loss strongly enhances the detrimental effects triggered by species introductions, pollution, climate change and hunting. Habitat loss is strongly tied with specific patterns of patch destruction, leading to habitat fragmentation (figure 1). Once fragmented into isolated patches, small discrete populations are much more vulnerable to extinction due to environmental fluctuations as well as demographic and genetic factors (such as inbreeding depression). The physical changes associated to habitat loss and fragmentation include reduction of total area and productivity of native areas, isolation of forest remnants and changes in physical conditions of the remnant fragments.

These antropogenic changes trigger further community responses that sometimes end in a biotic collapse. The sequence of biotic decay [33] includes initial exclusion of some species, deleterious effects of isolation and ecological imbalances. The later involve nonlinearities and cascade effects through the ecological

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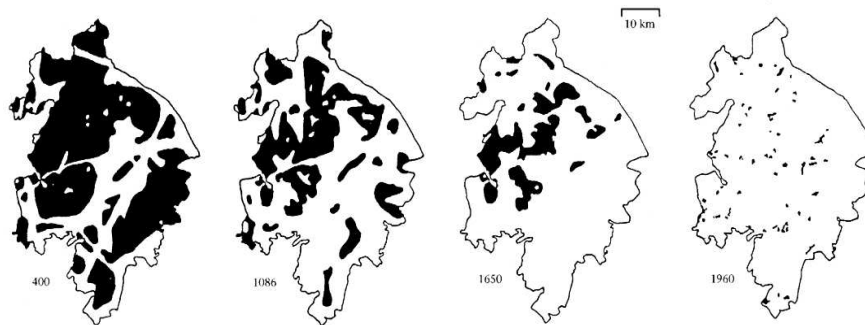


FIGURE 1 Temporal sequence of habitat loss and fragmentation in forests of Warwickshire, England. The sequence starts near A. D. 400 and ends in A. D. 1960. Extensive removal has taken place ending up with a scattered set of small patches.

webs. The loss of key species can promote subsequent loss of its predators, parasites or mutualists. One dramatic example (among others) is the so called *ecological meltdown* observed in predator-free forest fragments. The loss of predators generates strong imbalances shown by the disproportionate increase in the densities of prey and severe reductions of seedlings and saplings of canopy trees [29]. Conversely, the re-introduction of a previously removed predator can sometimes restore the previous biodiversity.

Human-induced habitat alteration is the major cause leading to biodiversity loss [31, 3]. Some authors have estimated an increase of the extinction rates by 1,000 times during the last 300 years, and they are comparable in magnitude to one of the five big mass extinction events [14]. Actually, some relevant differences between both events should be highlighted. In particular, previous mass-extinction events seem to be largely initiated by loss of diversity at the bottom layer of the networks (i. e. affecting primary producers). The current event is damaging webs at different levels. Primary producers are certainly being affected by habitat loss and degradation but keystone species (particularly large mammals) are being decimated too. Active, widespread hunting is reducing the populations of many species to red numbers. In this way, bottom-up and top-down cascades are unleashed. Habitat loss and degradation is often associated to tropical ecosystems, but it is a widespread phenomenon in all ecosystems. Even in the Antarctica, benthic ecosystems suffer strong disturbances due to iceberg movement damaging the sea floor [28]. Since these communities are known to grow very slowly, the increasing levels of ice breaking associated to global warming are severely damaging these communities.

Given the magnitude and consequences of habitat destruction, it is imperative to get enough insight to understand the effects of habitat loss on species

survival, and predict its further consequences. Since economic trade-offs are at play, scientist are oftentimes faced with the question of how much habitat can be destroyed before a certain species goes extinct. We start to get some data on the consequences of habitat loss, both using field observations [1, 2], and experiments [12, 23, 7]. While this approach is fundamental, it is hard to get enough information about the long-term consequences of habitat loss due to the large spatial and temporal scales at which this process takes place. For example, we can record the loss of species a few years after a human alteration, but there may be time lags [30]. Thus, other species still present may go extinct during the next years and so we may underestimate the effect of habitat destruction. In order to fully understand the consequences of habitat loss, models play a relevant role, particularly in forecasting the effects of landscape degradation on web structure and stability.

Theory suggests that the response of communities to habitat loss depends on both species' characteristics and the extent to which species interact. Larger-bodied and rare species are usually the first losers in most ecosystems around the world [34, 21]. Similarly, food web theory predicts that habitat loss and fragmentation reduces population densities of top predators [13], and therefore species from higher trophic levels are more frequently lost than species from lower levels (see [18] for a review). In a related context, the consequences of species loss are highly mediated by the position of such species within the interaction network [19, 24, 8]. The disappearance of preys attacked by numerous specialized predators, for example, have larger consequences than the loss of preys with fewer specialized predators.

In this chapter we have tried to synthesize this theory, highlighting new avenues linking habitat loss and food webs. Habitat destruction may yield qualitatively new consequences when considering species that are embedded in an intricate web of ecological relationships. Our belief is that advances in predicting the effects of habitat loss and fragmentation, and ultimately realistic estimations of extinction rates, would require considering the network of biotic interactions among species.

2 HABITAT DESTRUCTION IN LEVIN'S MODEL

The simplest, first approximation is obtained by exploring the consequences of habitat loss in a metapopulation. A metapopulation can be defined as a set of geographically distinct local populations maintained by a dynamical balance between colonization and extinction events. Let us start this section by revisiting the Levins' (1969) model, which captures the global dynamics of a metapopulation :

$$\frac{dx}{dt} = cx(1-x) - ex, \quad (1)$$

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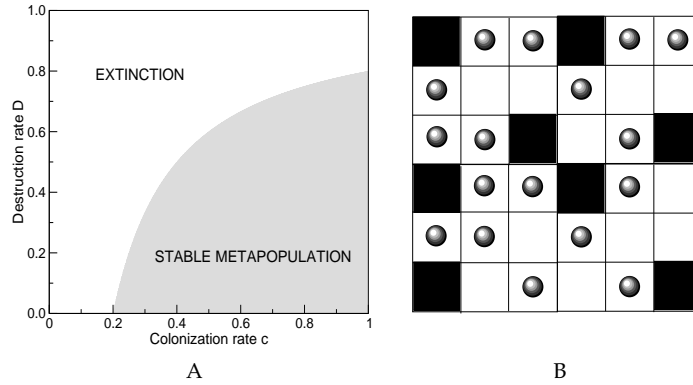


FIGURE 2 (A) Parameter space for the (spatially implicit) Levin's model, using a local extinction rate $e = 0.2$. Two domains are obtained from the transition curve $D_c = 1 - e/c$. This critical boundary separates the domain where a stable metapopulation exists from the extinction phase, where no metapopulation is able to persist. A discrete, spatial view of Levin's model would involve a set of patches (B) occupying a given domain. Here empty, destroyed and occupied sites are indicated as white, black and gray balls, respectively. The standard model assumes that all empty patches have the same probability of being colonized, whereas a more realistic scenario would consider colonization as a local phenomenon: only nearest occupied patches can colonize a given empty site.

where x is the fraction of patches occupied, and c and e are the colonization and extinction rates, respectively. This model has a non-trivial solution given by $x^* = 1 - e/c$. The colonization rate has to be larger than the extinction rate for the metapopulation to persist.

One can easily introduce habitat loss into the framework of model (1). If a fraction D of sites are permanently destroyed, this reduces the fraction of vacant sites that can potentially be occupied. Model (1) becomes:

$$\frac{dx}{dt} = cx(1 - D - x) - ex. \tag{2}$$

This model has two equilibrium points (to be obtained from $dx/dt = 0$): $x^* = 0$ (extinct population) and

$$x^* = 1 - D - \frac{e}{c} \tag{3}$$

This equilibrium point (3) decays linearly with habitat loss, becoming zero when $1 - D - e/c = 0$. This condition gives a critical destruction level D_c :

$$D_c = 1 - \frac{e}{c} \tag{4}$$

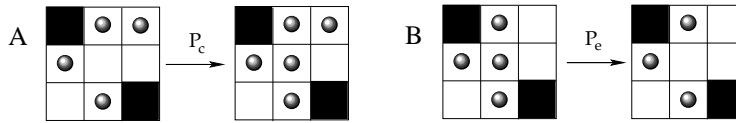


FIGURE 3 Local updating rules in a stochastic cellular automaton implementation of Levin's model. Here space is made explicit and the two basic events are colonization of empty sites (A) and extinction of occupied sites (B). These events have well-defined probabilities P_c and P_e , respectively.

indicating that a non-trivial dependence exists between available sites and the species-specific extinction and colonization properties. Once we cross this threshold (i. e. if $D > D_c$) the population gets inevitably extinct. This situation is illustrated in figure 2a. Here the critical line separating the two qualitative types of metapopulation allowed. Essentially, as we approach the critical value D_c by increasing the amount of habitat destroyed, the frequency of populated patches decays linearly, becoming zero at the boundary.

The main lesson to be extracted from this model is that (perhaps against our intuition) no sustainable metapopulation is possible once we reach a critical amount of habitat loss, in spite that a fraction of $1 - D$ patches is still habitable. The interaction between available areas and demographic parameters (here reduced to two local, average rates) leads to a threshold behavior.

Although Levin's model is a good approximation when dealing with metapopulations with long-range colonization, a more realistic view involves using a spatially-extended domain of available space and resources that can be colonized through local rules of death and dispersal. As more realism is introduced into the model, new important features become apparent. A specially interesting one is the effect of using a spatially explicit framework [4], such as the lattice shown in figure 2b. Now empty sites in the lattice (white patches) can only get colonized provided that at least one of the (four or eight) neighboring patches are already occupied.

The rules for the model are now local and stochastic and easily defined in probabilistic terms. In figure 3, we summarize the two basic rules to be applied. The first is colonization: an empty site will be colonized with a probability P_c proportional to the number of occupied neighbors (figure 3a). Extinction is simpler: a given occupied site becomes empty with some probability P_e , independently of the state of its neighbors. This spatial constraint strongly limits the dynamics of spatial occupation of a given landscape, and was shown to modify the predictions obtained from Levin's model, where all patches are equally available and thus global mixing is taking place. In particular, the predicted threshold for extinction becomes lower as the range of local colonization is reduced. Besides, spatial landscapes with random destruction of patches (here D would be the probabil-

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ity of a patch being non-available) display sharp thresholds: after a given D_c is reached, the largest connected patch suddenly becomes broken into many small sub-patches. Such a transition is sharp and strongly limits colonization even at high dispersal rates.

3 SMALL ECOLOGICAL WEBS AND HABITAT LOSS

One particularly important instance of ecosystem decay due to the propagation of habitat degradation to network structure is provided by the loss of top predators from fragmented habitats. It has been known from different available examples that after strong habitat reduction (either as a consequence of fragmentation or simple loss) top predators are likely to go extinct, unleashing a cascade of changes. This is well documented from the study of artificial islands resulting from the flooding of forests due to the building of dams.

One of the best known examples of ecosystem changes due to the creation of an artificial island is provided by Barro Colorado. The island was formed during the construction of the Panama Canal when the dam on the Chagres river was built and the water level rose, flooding the area that is now Lake Gatun. One direct consequence of the formation of Barro Colorado was the extinction of its most prominent top predator, the jaguar: *When jaguars and pumas disappeared from Barro Colorado (...) because the forest was no longer extensive to support them, the prey species soon increased tenfold. Effects of this shift in balance now appear to be rippling downward through the food chain. Coatis, agoutis, and pacas feed on large seeds that fall from the rain-forest canopy. When they become superabundant, they reduce the reproductive ability of the particular tree species that produce these seeds. Other species whose seeds are too small to be of interest of the animals benefit from the lessened competition (...). Over a period of years, the composition of the forest shift in their favor* ([32], pp.165).

How to introduce the importance of biotic (e.g. trophic) interactions in habitat fragmentation models? A good illustration of the importance of ecological interactions in enhancing the effects of habitat destruction is provided by considering a prey-predator metapopulation model (see [5] and references therein). It is a simple, but non-trivial extension of Levin's model. Here the predators can only live in patches occupied by prey. If x and y denote the fraction of patches occupied by prey and predator, respectively, the following model describes the trophic interaction:

$$\frac{dx}{dt} = c_x x(1 - x - D) - e_x x - \mu y, \quad (5)$$

$$\frac{dy}{dt} = c_y y(x - y) - e_y y. \quad (6)$$

Where again c and e are extinction and colonization rates, respectively. New terms have to be considered now. Prey mortality is decomposed in two terms:

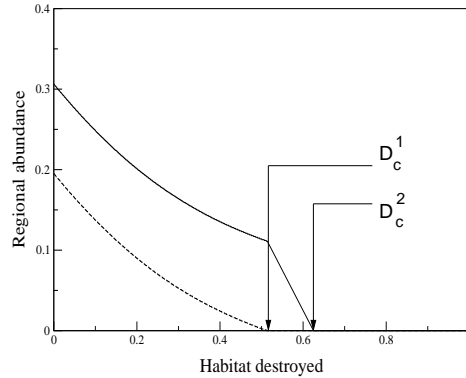


FIGURE 4 Equilibrium populations in the prey-predator metapopulation model when top-down control ($\mu > 0$) is considered. Here Prey's (solid line) and predator's (broken line) regional abundance are displayed against habitat loss D . Here we used: $\mu = 0.2$, $c_x = 0.4$, $c_y = 0.9$, $e_x = 0.15$, $e_y = 0.1$. The two arrows indicate the presence of two different extinction thresholds (see text).

they have a mortality rate e_x at patches where only prey is present (a fraction $x - y$ of sites). Additionally, it is further increased to $e_x + \mu$ in those patches where both prey and predator are present (a fraction y). Then, total mortality for prey is $e_x(x - y) + (e_x + \mu)y = e_x x + \mu y$. Available sites for predators are now the non-destroyed, empty sites occupied by prey (i.e., $x - y$) since predators are specialists and so they can not live without their prey. The model can describe different trophic interactions: donor control ($\mu = 0$) and top-down control ($\mu > 0$). This is important for two reasons. First, because theoretical models of trophic interactions have generally assumed scenarios in which natural enemies have a significant impact on prey populations (top-down control). Second, because donor control may operate in half of the parasitoid-host interactions, which in turn contain roughly half of the world's multicellular species [10].

The basic outcome of the model (see [5] for details) is shown in figure 4. Here the equilibrium populations of both predators (dashed lines) and prey (continuous line) are shown. The key result here is that two different thresholds of habitat destruction are shown to exist (arrows in figure 4). Below the first, $D_c^{(1)}$, both preys and predators coexist in the landscape. However, once the first threshold is reached, predators no longer exist. By further increasing habitat loss, prey are also extinct at the second threshold $D_c^{(2)}$.

Two relevant conclusions can be obtained from this study. The first is that extinction takes place first for the predator than for the prey. If predators are specialists we can expect a well-defined order in the pattern of extinctions, starting with the highest trophic level species and going down through the trophic

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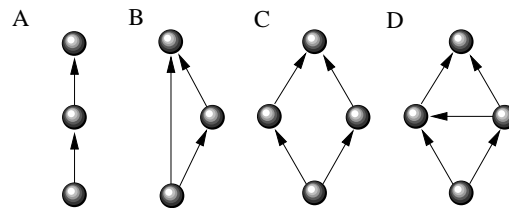


FIGURE 5 Basic food web modules analyzed in [?]. From bottom to top, plant, herbivores and top predators, with arrows indicating feeding links pointing from resources to consumers. A: simple food chain; B: omnivory (i.e. predator feeds both on herbivore and plant species); C: apparent competition (predator feeding on two herbivores), D: intraguild predation (one intermediate species feeds on the other).

chain. This may change if the predator is a generalist [27]. This means that habitat destruction is not only going to reduce biodiversity, but it will also reduce the length of the food chain.

A second, counterintuitive result also displayed in figure 4 is that the response of prey to habitat loss depends on the fraction of habitat which has been already destroyed. There are two different patterns of decay separated by $D_c^{(1)}$, the extinction threshold for the predator. When predators are present, prey abundance decays *slower* than when predators are extinct. Such result comes from the response to habitat loss, which is a trade-off between different trends depending on the trophic position. Thus, while habitat loss has just a negative effect for predators, prey face two opposite trends. On one hand their own habitat is reduced, which tends to decrease its regional abundance. On the other hand, habitat loss affects largely to predators, and so, reduces predation pressure, which tends to increase prey regional abundance. Once predators go extinct, the trade-off between the two opposite forces disappears, and prey abundance decreases much faster with additional habitat loss. Thus, the rate of decrease depends on the amount of habitat already destroyed.

A more detailed exploration of this problem was done by Melian and Bascompte [16] using Pimm's basic modules (figure 5). They showed that the sensitivity of the top predator to habitat loss depends on the food web module to which it belongs. In particular, omnivorous predators (figure 5B) are more resistant to habitat loss than predators embedded in other types of food web modules. Also, the extinction threshold of predators is lower for top-down control than for donor-control, but this difference attenuates with decreasing trophic level. Whether predictions arising from food web modules scale up to more complex communities needs further testing.

All these results based on simplified food webs indicate that the pattern of species interactions is a key ingredient in ecosystem's responses to habitat loss.

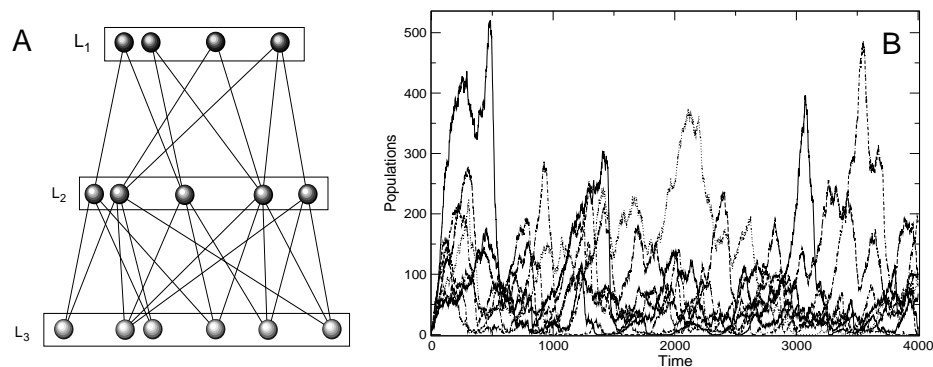


FIGURE 6 Spatially-explicit, 3 trophic-level model of many species interactions. The model is a general framework for simulating the dynamics of multispecies ecosystems in a fragmented landscapes. Network structure (A) is easily defined through a matrix of weighted interactions connecting producers, herbivores and predators (here indicated as light, dark and darker gray balls, respectively). In the version presented here, omnivory is not considered. The model exhibits complex dynamics, with fluctuations in population numbers and species turnover (B).

The next step requires going beyond small, predefined subgraphs and exploring the full complexity of rich multispecies assemblages.

4 ECOSYSTEM MELTDOWN UNDER FRAGMENTATION

In order to understand the whole impact of habitat loss and fragmentation on complex ecosystems, we need to explicitly consider both species diversity and spatial constraints. Predicted diversity losses as habitat destruction increases with time rely on species-area relations [20]. But the structure of ecological networks has been shown to be no less important [24, 8]. Additionally, models should consider the possibility of immigrating species from regional pools as well as species turnover.

The effects of habitat loss in complex, multispecies food webs is explored here by means of a stochastic spatial model comprising three multispecies trophic levels. We will extend a previous framework [25, 15] defined by a simple model of species interactions which has been shown to display most of the statistical properties characteristic of diverse communities. These include species-abundance relations, connectance-species stability curves, species-area patterns and other relevant dynamical properties [26]. The model considered here is an example of an interacting particle system [9]. Here a two-dimensional lattice $N = L \times L$ available sites is considered, together with a pool $\Sigma(S)$ of possible species. Each

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site can be occupied (or not) by a single individual of a given species. Sites are assumed to be identical, except for the binary distinction of available or destroyed. Interactions among individuals are introduced through a random matrix Ω , and the strength of species interactions is drawn from a uniform distribution. This matrix is fixed and has a predefined connectivity C .

In our setting, we consider three trophic levels. The set of all species in a regional pool, $\Sigma(S)$, is defined as

$$\Sigma(S) = \{0, 1, 2, \dots, S\}, \quad (7)$$

where 0 indicates empty space. Here we consider three trophic levels (figure 6a). The previous set will be subdivided into three classes plus empty spaces:

$$\Sigma(S) = \{0\} \cup \Sigma_1(S) \cup \Sigma_2(S) \cup \Sigma_3(S) \quad (8)$$

with the three levels having the same numbers of (potential) species per level:

$$\Sigma_1(S) = \{1, 2, \dots, [S/3]\}$$

$$\Sigma_2(S) = \{[S/3] + 1, \dots, [2S/3]\}$$

$$\Sigma_3(S) = \{[2S/3] + 1, \dots, S\}$$

(here $[x]$ indicates integer part). The following rules are then applied:

1. Immigration: an empty site 0 is occupied by a species randomly chosen from the set of (non-empty) species with probability μ , i.e. $A \in \Sigma(S) - \{0\}$:



For simplicity, we use the same immigration rate for all species. Here, we take $\mu = 10^{-4}$.

2. Death: All occupied sites can become empty with some fixed probability e_i :



here the same probability is applied to all species, with $e_i = e = 0.02$.

3. Colonization of empty sites by plants: plants can occupy empty sites by colonization, as defined in Levin's model. Here a given species $A \in \Sigma_1$ will occupy a neighboring empty site,



with some probability of colonization c .

4. Biotic interactions: pairs of individuals belonging to different species will interact through a probabilistic community matrix Ω . The entries of this $S \times S$ matrix are the probabilities of pairwise interactions. Such interactions are defined in terms of rules: two species $A, B \in \Sigma(S)$ having non-zero entries

Ω_{AB} can interact, provided they are nearest neighbors. Given the three-layer structure of the community under consideration, three different cases need to be considered. The first set are competitive interactions among species within $\Sigma_1(S)$. A given individual from species i will invade a neighboring patch occupied by a different species j

$$P_{ij} = \pi[\Omega_{ij} - \Omega_{ji}] , \quad (12)$$

where $\pi[x] = x$ when $x > 0$ and zero otherwise. This probability of an interaction occurring in the system between species i and j is a measure of the interaction strength linking these species.

Interactions between levels $1 \leftrightarrow 2$ and $2 \leftrightarrow 3$ are also defined in terms of probabilistic rules. For example, a predator $B \in \Sigma_3(S)$ will prey on a site occupied by a species $A \in \Sigma_2(S)$ with probability Ω_{AB} . In this context, propagation of predators through space requires the presence of their prey. If $\Omega_{AB} = 0$, no expansion will take place. The same rule applies to pairs of species $C \in \Sigma_2(S)$ and $D \in \Sigma_1(S)$.

For a very small, $S = 9$ pool, the structure of the matrix used in our model is a block matrix with a well-defined structure:

$$\Omega = \begin{pmatrix} w_{11} & w_{12} & w_{13} & 0 & 0 & 0 & 0 & 0 & 0 \\ w_{21} & w_{22} & w_{23} & 0 & 0 & 0 & 0 & 0 & 0 \\ w_{31} & w_{32} & w_{33} & 0 & 0 & 0 & 0 & 0 & 0 \\ \\ w_{41} & w_{42} & w_{43} & 0 & 0 & 0 & 0 & 0 & 0 \\ w_{51} & w_{52} & w_{53} & 0 & 0 & 0 & 0 & 0 & 0 \\ w_{61} & w_{62} & w_{63} & 0 & 0 & 0 & 0 & 0 & 0 \\ \\ 0 & 0 & 0 & w_{74} & w_{75} & w_{76} & 0 & 0 & 0 \\ 0 & 0 & 0 & w_{84} & w_{85} & w_{86} & 0 & 0 & 0 \\ 0 & 0 & 0 & w_{94} & w_{95} & w_{96} & 0 & 0 & 0 \end{pmatrix} \quad (13)$$

Only some non-zero values are possible: the allowed matrix elements are filled with (connectance) probability C . Notice that here connectance also includes competitive interactions among plants, and therefore its values will be typically higher than those observed in real food webs.

The model exhibits complex dynamics, including wide time fluctuations and (for small numbers of species) deterministic chaos. An example of the time series generated by the previous rules is shown in figure 6b. Since we allow immigration (and thus potential invaders) to occur, as well as extinction, species turnover takes place.

In figure 7 we show an example of the network changes that take place in a $S = 300$ system with $C = 0.13$, $\mu = 10^{-4}$, $L = 200$. Here we start from a random

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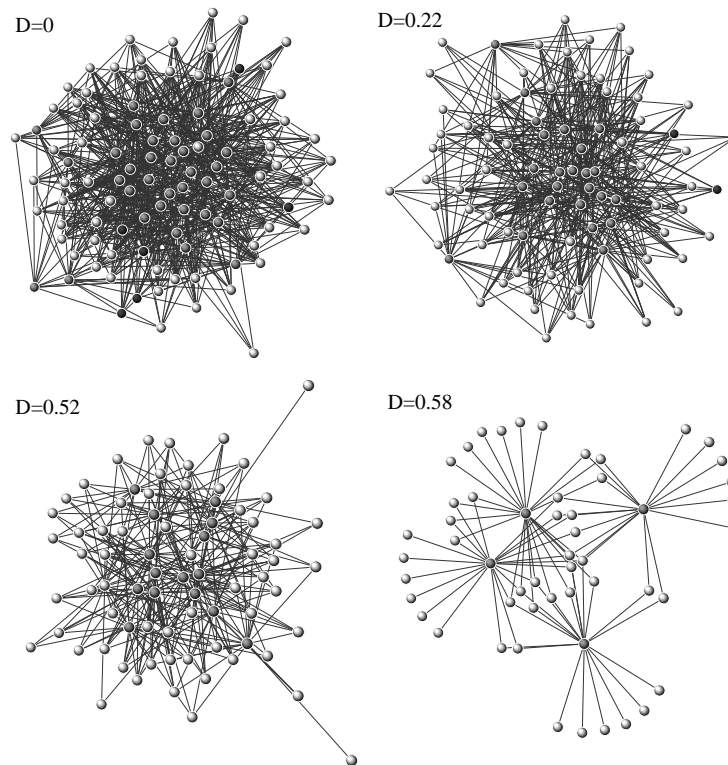


FIGURE 7 An example of the changes occurring in the web structure of the multispecies, three trophic stochastic model. As habitat destruction increases, predators decay first, with a transient increase in herbivores followed by further decay of them. Eventually, as herbivores are gone, an increase in the number of plants is observed, followed by a final crash for large enough destruction levels. Producers, herbivores and predators are indicated as light, dark and darker gray balls, respectively.

initial condition and plot the network of trophic interactions (thus excluding competition) at some given step. In these pictures only the largest connected component is shown. For no destruction ($D = 0$) we find a network where the three levels are represented. As habitat loss increases, the network starts losing mainly top predators. The time series of population changes after the loss of some of these predators reveals wide fluctuations (particularly in herbivore populations) over a transient period of time. At $D = 0.22$ only two predators remain and for $D = 0.52$, no predators are present. At this stage surviving herbivores tend to be generalists. Such tendency rapidly increases as D is further increased.

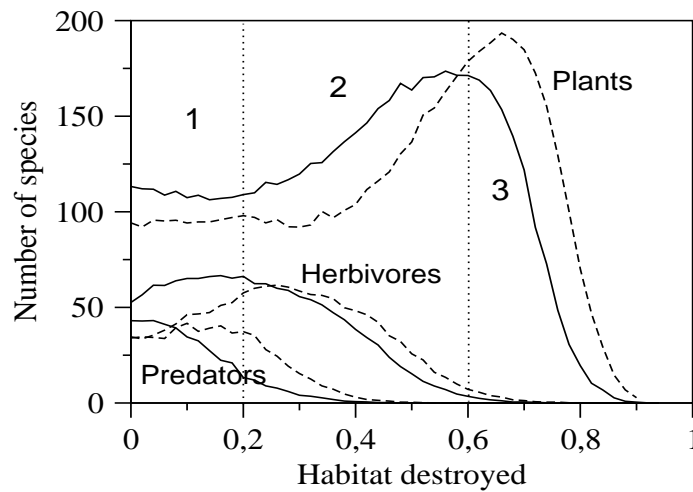


FIGURE 8 Number of species in each trophic level for different values of habitat destroyed. Here two different probabilities of colonization by plants are used: $p = 0.15$, straight lines; $p = 0.25$, dashed lines). Three different regions are defined and separated by dotted lines (numbers in the figure). See text for details. Other parameters: $C = 0.28$ (including competitive interactions among plants).

For $D = 0.58$ only four highly connected (i. e. generalist) herbivores are left. A slight increase in habitat loss triggers the extinction of all of them. Beyond the transient dynamics revealed by population changes over time, we can look at ecological meltdown in a broader perspective. By increasing habitat destruction in the stochastic model, we analyse how biodiversity is changed in terms of the number of species present.

Our model shows that as habitat destruction increases, predators are lost first, then herbivores and finally producers. But the interaction between trophic levels yields very interesting outcomes not predicted when a single trophic level is observed alone. In Figure 8 we can observe three different regions. The first region ($D < 0.2$) is characterized by a quick decline in predator species richness and consequent increase in herbivores and decrease in plant richness, corresponding to a typical trophic cascade. For high colonization rates of plants, predators start declining later, and, more interestingly, the trophic cascade is not observed, that is, plant richness does not decrease as herbivores release from their predators. Our results suggest that trophic cascades triggered by habitat loss are more frequent when plant colonization is low or reduced by other factors (e.g. climate change). The second region ($0.2 < D < 0.6$) is characterized by the decrease in herbivore richness and quick drop in plant richness. Indeed, the maximum values for plant richness are observed within this region, together with predator-free

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ecosystems. The third and last region corresponds to the collapse of the plant assemblage ($D > 60$), because colonization is not enough to compensate for habitat destruction. These results are robust to both the spatial scale considered (we have used different lattice sizes) and the richness of the regional pool.

Our models shows that predator-free ecosystems can maintain numerous herbivores and plants. However, we believe this might be only true when interactions between plants and the second trophic level are mainly antagonistic (i. e., trophic, parasitic). When positive interactions between both trophic levels are more frequent than negative ones (i.e. when mutualistic interactions like dispersal and pollination are stronger and more frequent than feeding links), this particular result would not be observed. In this case, plant colonization rely upon herbivore dispersal, and therefore the dynamic behavior of plant richness would be similar to that of dispersers, and ecosystem collapse might occur earlier. Further developments on our model will introduce these mutualisms for predicting different biodiversity collapse scenarios depending on the relative importance of antagonistic and mutualistic interactions. Interestingly, mutualisms become more frequent in comparison to feeding links as we move towards the tropics, suggesting critical thresholds might be achieved faster in these ecosystems.

5 DISCUSSION

Habitat loss and fragmentation is, together with species invasions and climate change, the main player responsible for the current extinction event. Degraded habitats lead to species loss and the success of exotic species. Climate change is slowly modifying the distribution ranges of many species and indirectly the spatiotemporal patterns of ecological networks. The synergies between habitat loss and fragmentation, climate change and network architecture are barely known today, and models can help to forecast possible scenarios of future biodiversity loss.

Previous studies on species removal in food webs ([19, 24, 8]) have been concentrated in ecological networks lacking spatially-explicit components. But all of them reveal that some species play a particularly relevant role in maintaining network stability. One important question here is how much affected are these keystone species by habitat loss and fragmentation. Is habitat loss specifically affecting them? This seems to be the case of many vertebrates [29, 32] and is well exemplified by its effects on army ants. Army ants [11] are known to have a great impact in neotropical rainforests. Many species of vertebrates and invertebrates associated to them will face extinction if the army ants disappeared [6]. Given their special patterns of spatial search through the forest floors, involving search over wide areas, they have a huge impact on the spatial and temporal distribution of their ecological partners. Army ant raids facilitate species diversity through by altering local ecological succession, creating a spatial mosaic of habitat patches. [17]. Additionally, in some rainforests a large number of bird

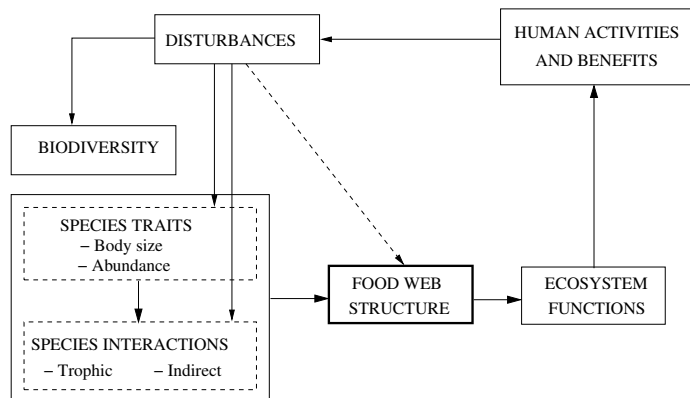


FIGURE 9 Conceptual summary that may guide future models aiming to integrate disturbances and ecological networks. Here food web structure emerges from the interaction between biodiversity (i.e. species richness), species traits (e.g. body size) and species interactions. These food webs support some of the functions and services provided by ecosystems. Humans, as part of the ecosystem, are benefited and can develop different types of activities, some of them beyond the resilience of the ecosystem. These disturbances may affect biodiversity in general, species with particular traits, or species interactions. This can promote further changes in food web structure and functioning, ultimately affecting our activities.

species are specialized in following their raids, feeding on insect prey that are flushed out from leaf litter. The analysis of the effects of habitat fragmentation, reveals that their populations would get extinct once destruction thresholds are reached [6].

Our analysis of multispecies ecosystems indicates that the effects of habitat loss combine with those associated to network structure in predictable ways. The pattern of species loss affects plant species directly through the loss of available space, but the trend (in terms of the total number of species present) can be reversed as top predators and herbivores experience diversity decay. Top predators are particularly affected by loss of habitat, as observed from field studies. Our study predicts that the demographic patterns of herbivore increases due to ecosystem meltdown are actually also present at the species level: the decay of diversity at higher levels is followed by an increase in herbivore diversity at intermediate levels of destruction. In this domain, plant diversity slightly decreases. Once habitat loss starts to trigger the decline of herbivores, a rapid increase in plant diversity is observed. This is actually an interesting counterpart of the explosion of herbivore populations following the loss of top predators. Under our approximations, it is predicted that plant diversity will raise once freed from grazing pressure. This is of course limited by the important role

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played by mutualistic interactions associated with species in other trophic levels. Such interactions should be included in future models of community dynamics.

Different extinction patterns have different effects on ecosystems, and they ultimately determine changes in network structure and ecosystem functioning (e.g. [22]). It is therefore crucial to identify the route to extinction triggered by different disturbances, addressing whether they primarily affect biodiversity in general (i.e. random extinctions), species with particular traits (e.g. body size, temperature tolerance), or species interactions (e.g. via spatiotemporal changes). It is time to incorporate more realistic extinction patterns into more realistic models, and the integration of multitrophic complex communities and habitat loss presented here is an example of how to achieve this goal.

ACKNOWLEDGMENTS

The authors thanks the members of the CSL for useful discussions. This work has been supported by a FIS2004-05422 and REN2003-03989 grants and by the Santa Fe Institute.

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