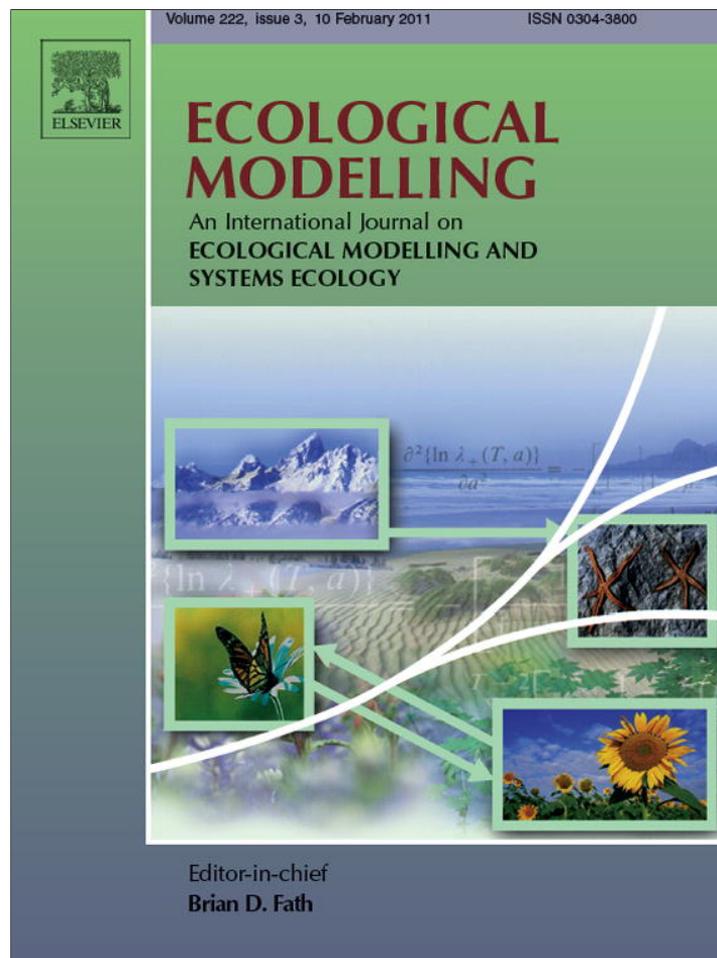


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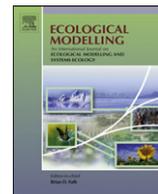
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Connected fragmented habitats facilitate stable coexistence dynamics

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ABSTRACT

In this paper we endeavor to test the controversial ideas that exist about the role of fragmentation in a conservation context. In line with earlier understanding, we find that habitat fragmentation alone results in a strong detrimental effect (especially for the predator population). Connecting the fragmented habitats facilitates predator survival and hence prey survival as compared to the unconnected fragmented case. Our main result is counterintuitive: in the presence of a high quality predator, connected fragmented habitats ensure a better chance for coexistence than does even the unfragmented case. We explain why a connected fragmented habitat might thus be beneficial for the stabilization of the system, and how connections between sub-habitats are able to protect prey population from over-exploitation. In the model, habitat fragmentation is separated from the effects of habitat destruction, in order to better understand how populations react to habitat transformation.

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1. Introduction

In this paper we study how habitat fragmentation and the connection of the fragmented habitats affect the dynamics and survival of animals in a simple model system. In a simulation model of a tri-trophic predator–prey system we show that:

- fragmentation has a detrimental effect, especially on predators;
- connecting fragmented habitats stabilizes both predator and prey populations;
- connected fragmented habitats yield the coexistence of predator and prey above the level of an undivided, unfragmented habitat.

The first statement confirms common expectation. The second extends related findings from host-parasitoid dynamics (Visser et al., 2009) or about the stabilizing effect of spatial decoupling on predator prey systems (e.g., De Roos et al., 1991; Savill and Hogeweg, 1999). The third result is counterintuitive and requires careful elaboration. The purpose of this paper is to establish the above results, and to back them up with methodology, simulation results, and analysis.

Habitat fragmentation, the process of subdividing a habitat into smaller areas, occurs in natural systems via fire, flood and other natural causes. However, the most important type of habitat fragmentation is due to the expansion and intensification of

human land use (Burgess and Sharpe, 1981). Conservationists seek insights from ecological theory to select strategies of habitat management that will best maintain threatened species. The issue often revolves around how to assess dangers posed by habitat fragmentation. Habitat fragmentation affects numerous ecological processes across multiple spatial and temporal scales, including shifts in habitat use, changing population dynamics, and altering species compositions (Schweiger et al., 2000). Despite the ubiquity of fragmentation and the great interest expressed by ecologists, there is a difficulty in answering even some of the most important questions (Harrison and Bruna, 1999). When a given habitat undergoes fragmentation, the change in spatial configuration typically also coincides with the reduction of the size and quality of the habitat. Documenting the ecological effects of habitat loss, however significant, does not convey much information about the changes of the spatial structure introduced by fragmentation alone (Franklin et al., 2002). Therefore, to assess the influence of natural habitat fragmentation, the effects of habitat loss and habitat fragmentation should be treated independently (Fahrig, 2003). In this paper we define a fragmented habitat as a habitat where the original area is separated into smaller parts via impassable borders (or borders with narrow openings), and we study the effects of isolated or connected fragments without habitat loss. This approach allows us to focus on a single aspect of habitat fragmentation, namely, compartmentalization.

1.1. Background

The popularity of corridors in conservation biology stems from the intuitive relationship to their purported function by physically

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connecting isolated habitat fragments. Corridors are expected to increase population viability via offsetting local extinction, but also, because of their restricted physical throughput, corridors might delay migration. These delays can be very important when a heavily predated population migrates into an area in the original habitat network where there is no predator at the moment (e.g., where predators became extinct or their numbers are extremely low) and these areas provide a temporal refuge for the prey. Corridors can also be beneficial to the predator population. Beier (1993) observed, through modeling studies, that the presence of a corridor allowing even low levels of migration has improved the probability of survival of a cougar population in Southern California. General spatial models in ecology, including island biogeographic models (MacArthur and Wilson, 1967) and metapopulation models (Levins, 1969; Caswell and Cohen, 1991; Hanski, 1999) predict that movements between patches will increase population size and persistence. These habitat shifts are common consequences of how populations react to changing environments (Gyorffy and Karsai, 1991; Karsai et al., 1994).

The study of the effects of corridors on population viability as well as the empirical understanding of corridors' effects on community structure is still in its infancy (McKenzie and Bio, 1995). Haddad and Tewksbury (2006) reviewed major ecology and general science journals from 1997 to 2003 to find only 20 studies to test corridors' effects on populations or diversity. They concluded that the current evidence offers only a tentative support for the positive effects of corridors, and that much more work on population and community responses is needed, especially, that it is important to study the mechanisms and conditions under which we can expect corridors to impact populations. They also predicted an increasing importance of individual based models that complement empirical studies by focusing on the effect of different life history parameters (Haddad and Tewksbury, 2006). The study of fragmentation seems to be controversial: "despite extensive empirical research and previous reviews, no clear patterns regarding the effects of habitat loss and fragmentation on predator–prey interactions have emerged" (Ryall and Fahrig, 2006). Ryall and Fahrig emphasize the importance of theoretical predictions (and hence of computational models) in assessing the effects of fragmentation in predator–prey systems.

In this paper we present a minimalist individual based model to study how fragmentation (without habitat loss) and the reconnection of the habitats by opening connections influence the stability of a simple predator–prey system. Individual based modeling has become a widely used tool for describing complex systems made out of autonomous entities (DeAngelis and Mooij, 2005; Grimm et al., 2006). As opposed to most aggregate models, individual based models allow the use of spatially explicit predation processes and simple stochastic mechanisms for the organisms to find food and new habitats. In our model, only consumption, reproduction, and predation are assumed at the individual organism level. Density dependent effects and other aspects of dynamics arise as emergent consequences of the context-independent individual interactions that generate spatiotemporal structures in the model habitat. Our goal is to show that the interconnectedness of the fragments can stabilize prey predation dynamics under various conditions. The model is described using the ODD protocol advocated by Grimm et al. (2006).

2. Materials and methods

2.1. Purpose

The purpose of the model is to understand how fragmentation and the re-connection of the fragments affect predator prey

Table 1

Model parameters and initial values used in the simulations.

Parameter	Notation and value
Starting number of prey	$N_{PY} = 1000$
Starting number of predator	$N_{PD} = 100$
Corridor width	$\sigma = 3$
Wall thickness	$w = 2$
Motion speed	$Fd = 0.9$
Prey energy gain	$Gain_{PY} = 4$
Predator energy gain	$Gain_{PD} = \text{varied } (10, 30, 50, 70)$
Initial energy max. prey	$E_{PY} = 2 * Gain_{PY}$
Initial energy max. predator	$E_{PD} = 2 * Gain_{PD}$
Area linear dimension	$n = 200$
Fertility	$R_{PY} = R_{PD} = 15\%$
Regeneration time	$K = 5$
Max. turning	$T = 50$
Test interval t	$t = 50 - 10,000$

systems, in particular in terms of coexistence. For simplicity, we confine the present study to a tri-trophic model consisting of a non-mobile resource, a prey feeding on this resource, and a predator.

2.2. State variables and scales

The model ecosystem consists of a varying number of autonomous predator and prey individuals whose dynamics is entirely controlled by the individuals' behavior. Predation is obligate. Both predators and prey are consumers, that is, they feed on biotic (replicating) resources. Prey food simply regenerates after a time, while prey itself replicates according to its individual energy budget (Fig. 2). The system therefore shows many similarities to the experimental microcosm experiment of Holyoak and Lawler (1996) where bacteria for the bacterivorous *Colpidium* were provided as a renewable resource and the bacterivorous ciliate was consumed by another ciliate, *Didinium*. Prey food has an autonomous growth dynamics that leads to saturation (such as in the case of bacteria in a Petri dish, grass on the meadow, or plankton in the sea).

The model is a spatially explicit, individual based system, consisting of $n \times n$ spatial locations (Table 1 specifies the relevant parameters). The habitat is modeled as a rectangular area with reflecting boundaries. Each position except the borders can be empty or occupied by an arbitrary number of individuals (except for prey food which can exist at a certain position or not at a given moment). In other words, locations are assumed to represent small finite areas where more than one individual can live, rather than spatial points of zero extension. Fragmentation is implemented by placing borders with reflecting walls into the habitat. These narrow walls (similarly to real roads, canals, fences or other hard boundaries) do not decrease the total habitat size significantly, in harmony with our goal to separate habitat loss from fragmentation (wall width is minimal and the area loss to walls is 2–4% in the studied situations). Walls are impassable for the organisms and behave the same way as does the outer boundary. Connections between fragments are implemented as openings in the walls, where organisms can pass through freely. The openings are large enough to permit multiple organisms to cross at the same time (Fig. 1). In this study, the openings differ from real life corridors in that they have no length parameter or any other special properties that impede or promote migration or survival. We deliberately simplified the corridors into simple openings where animals can easily pass into another sub-habitat, so that we can focus on one single factor, namely, the different degrees of connectedness of sub-habitats.

The behaviors are converted into a single common currency, "energy". Energy is the state variable related to the well-being condition of the individual: it expresses the level of food and the expected lifetime of the organism. In the practical setting of the model experiments (to cut ahead of the details) the linear size of

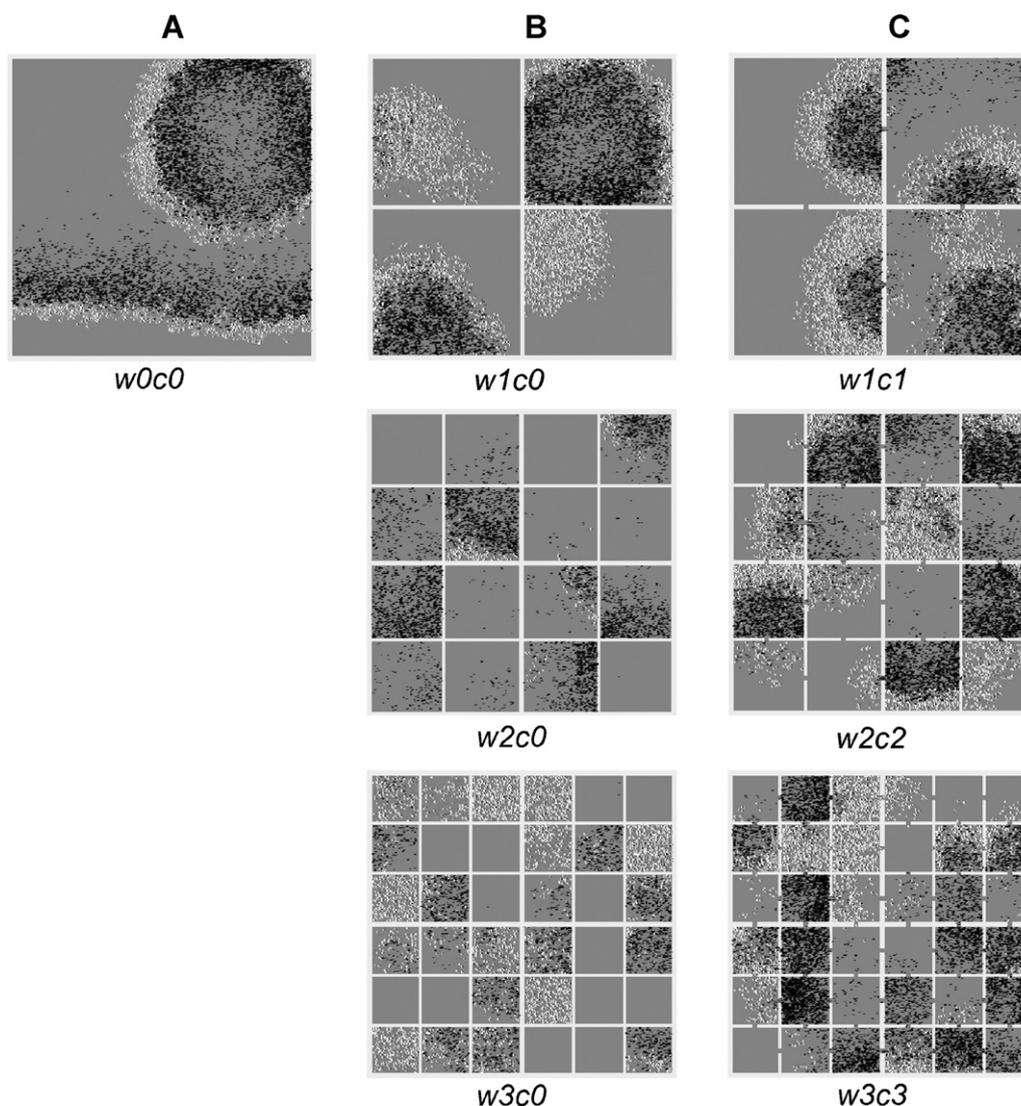


Fig. 1. Fragmentation schemes studied in this paper: $wXcY$ is an X walls and Y connectors (openings) system. Basic habitat setups: (A) unfragmented habitat (left column); (B) fragmented habitat (middle column); (C) connected fragmented habitat (right column). Light dots: prey and dark dots: predator.

the field n was assumed to be 200, whereas the spatial size of the individuals and migration speed to be 1: thus, for instance, if we assume one time tick to correspond to one day, this means an overall area linearly explorable (from end to end) in about 7 months. The area is therefore assumed to be large enough to capture large-scale spatiotemporal dynamics akin to that found in real ecosystems.

2.3. Process overview and scheduling

At each discrete time step, a given list of actions is performed in a sequential order, which consists of predator, prey, and prey food operations. In each turn, every individual (activated in a dynamically randomized order) carries out the following sequence of actions: move randomly in physical space, consume available resources if possible, reproduce by chance, and die, if energy is out (Fig. 2).

The agents' velocity Fd is constant for both the predator and the prey. Each move occurs in a randomly selected direction, taken uniformly from the interval $\pm T$ (the degree of turning in degrees relative to the current momentary orientation of the given individual, and represented on a continuous scale).

Prey individuals feed by consuming a food token at the same location (i.e., in the same small area represented as one location

in the model). As in real life, food is consumed only if available. Similarly, the predator feeds by consuming a single prey individual in the same fashion. Upon consuming an individual, the consumer receives a certain amount of "energy", which is $Gain_{py}$ and $Gain_{pd}$ for the prey and the predator, respectively. The consumed individual dies and is removed from the system.

Reproduction is asexual and occurs with a fixed probability (R_{py} and R_{pd} , for prey and predator, respectively). Upon reproduction, a new individual of the given type is produced at the spot of the parent but with a random spatial orientation (i.e., a random direction of initial motion). The energy reserve of the parent will be shared evenly with the offspring. The reproduction of prey food is different: it simply regenerates in K steps.

Death happens by consumption (for the prey), or if the energy level of the individual reaches zero. An energy discounting operation is used that removes one energy token from each prey and predator individual per every time step (thus, "energy" directly translates to the available lifetime of prey and predator individuals, expressed in time ticks; also, in this way one step of motion costs one unit of energy).

The model was developed in the NetLogo simulation environment (version 3.15). Inspiration for the simple predator system was gained from Wilensky (1998, 1999) and Jacobson and Wilensky

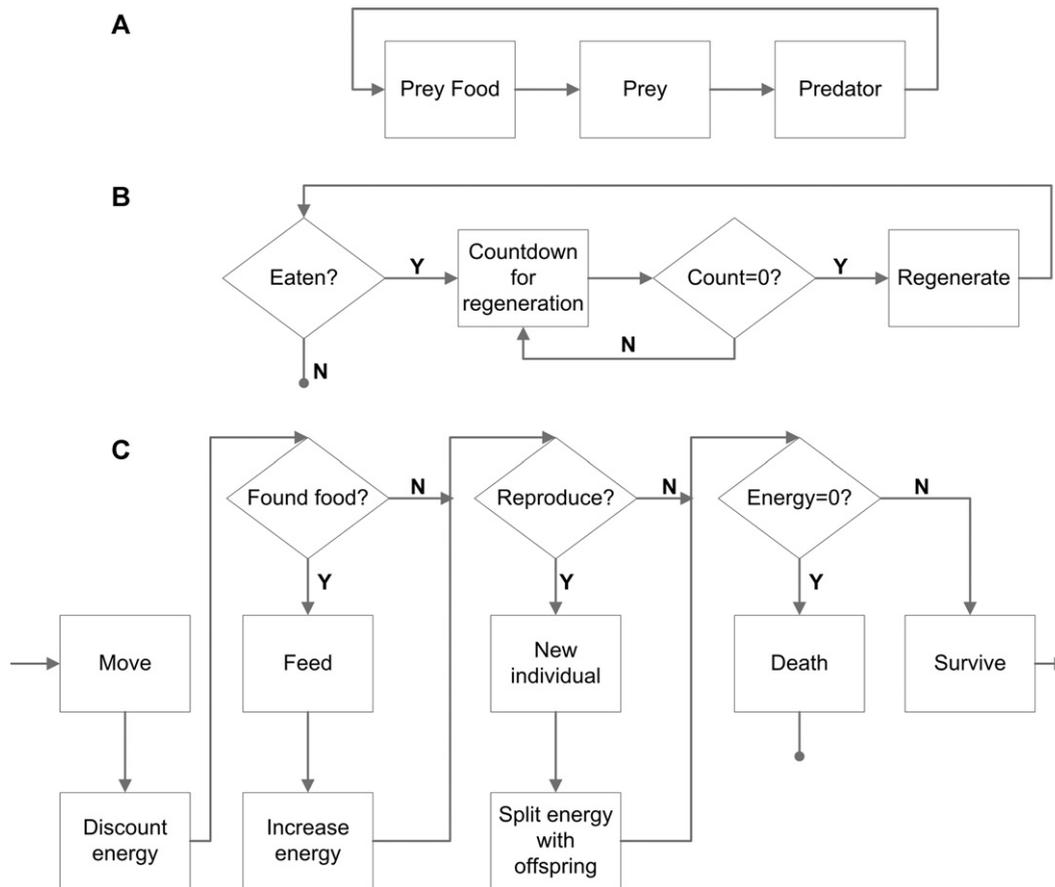


Fig. 2. Process overview of the model. (A) Basic cycle of the tri-trophic model; (B) growth cycle of the prey food; (C) activity and energy model of both prey and predator.

(2006); the fully functional model and the source code are available at <http://kampus.web.elte.hu/models/HabitatFragmentation.nlogo> and at <http://ccl.northwestern.edu/netlogo/models/community/HabitatFragmentation>. (All code is the work of the present authors.)

2.4. Design concepts

Emergence. The model's population dynamics, aggregate behaviors and some individual behaviors emerge from the interaction of the individuals. The number and position of predator and prey, as well as (on a different scale) spatiotemporal patterns of the organisms' distribution, but also the lifetime of individuals are all consequences of the iterated dynamics of the system, fully controlled by the individuals' properties and stochastic rules. For example, food seeking is controlled by random walk, and lifetime is controlled by consumed food (i.e., energy), as a contingent consequence of the success of finding food, etc.

Interaction. Interaction takes a single form: simplified predation, which is understood as energy transfer (from the consumed to the consumer). We do not consider conversion rates and other details in the model. More than one individual can occupy the same spatial position, but a prey individual can only be consumed by a single predator.

Sensing. Predators "sense" prey only by contact, i.e., by assuming an identical spatial position (we repeat that spatial positions are discrete and represent small areas). Area borders, walls, and openings are not fore sensed but stumbled upon in a random walk.

Stochasticity. We use the high quality built-in random number generator of the simulation platform. Stochastic events are birth by

reproduction (asexual) and spatial motion (composed of a deterministic forward component and a random direction).

Observation. The model comes along with a GUI for visual inspection (e.g., 2D spatial plot of the individuals in the field). The following information has been monitored on the screen and saved into a file for further data processing: all model parameters, random seed value, the number of individuals at each time step for both predator and prey, and phase volume. Phase volume (detailed later) is the state space volume spanned by the difference between maximum and minimum numbers of the prey and predator individuals, respectively, for a time interval large enough to contain several population oscillations. Together, these items are the kind of data field ecologists might also find easy to collect.

2.5. Initialization

When the system is initialized, prey food is brought into a saturated state and a number of N_{PY} prey and N_{PD} predator individuals, respectively, are placed randomly into the habitat. Prey and predator start with random orientation and receive a randomized amount of initial energy (between 0 and E_{PY} and E_{PD} , respectively).

The starting point of our analysis was selected during pre-experiments. The applied baseline setting defines an initial area which is large enough to support a high density population of about 10,000 individuals of prey and predator alike at the given values of parameters (Table 1.). Under these conditions, in the unfragmented area ($w0c0$) the prey population always persists indefinitely without predators, while prey and predator tend to coexist (i.e., both survive) in the time interval considered.

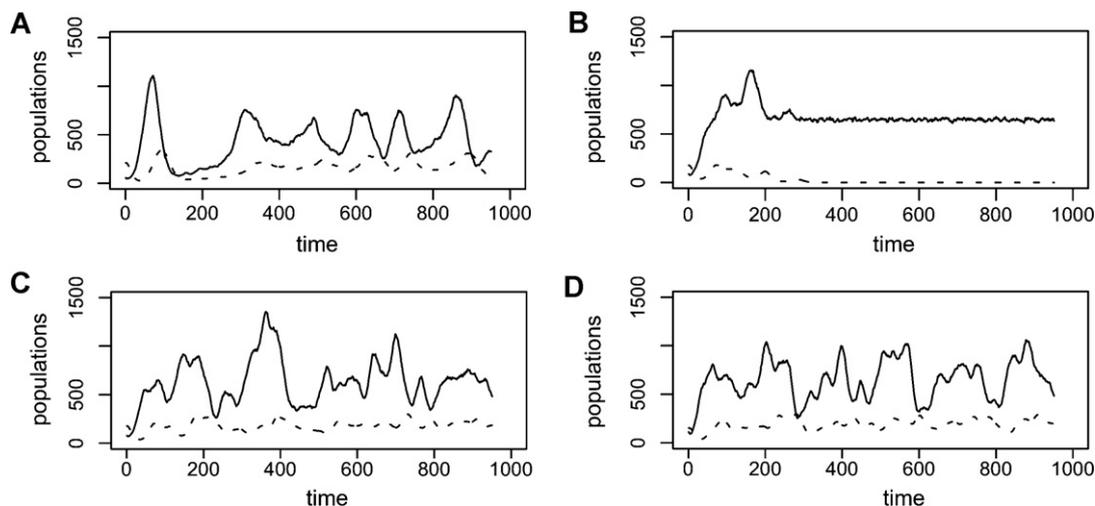


Fig. 3. Sample time plots for $Gain_{PD} = 50$. (A) Unfragmented ($w0c0$), (B) fragmented ($w2c0$), as well as two different fragmented connected systems (C: $w3c3$ and D: $w2c2$). Solid line denotes prey, dashed line denotes predator. Population numbers are shown as per unit energy (i.e., relative to energy content in the organisms in order to normalize for the longevity of predators). Time frame shown is $50 < t < 1000$, i.e., 950 time steps, discarding initialization dynamics as detailed in the text; eventual survival times in the lower row (fragmented connected system) are higher (see also Fig. 4).

2.6. Submodels

We studied various arrangements as depicted in Fig. 1. The main control parameter of the model is the number of walls and openings. With this, we generate different fragmented (viz. fragmented and connected) habitats. By setting these combinations to various values, we want to understand the difference between the behaviors of predator and prey populations in the various types of habitats.

Within the given framework, we use different types of predators to assess their effects on the system. This at the same time provides a kind of sensitivity testing for the main control parameter. The numerical value used to define the different predators is $Gain_{PD}$, which is the energy gain for the predator when a unit of prey is consumed. This parameter is used here as an umbrella descriptor for many direct and indirect relationships between several life history parameters. For example, in reality predators are typically larger, move faster and cover a larger area for food than do their prey. We note that predators and prey move and forage at the same speed in this model. Instead of using different movement patterns, searching strategies, we embedded these life history differences into the energy budget. Predators gain more energy from food, which means that they can move farther and explore more area before starvation. High levels of predator gain and hence higher levels of accumulated energy reserves of the predators tend to imply increased expected predator lifetimes, which in turn can be interpreted as dealing with a fast moving and efficient natural predator that controls a large area. The same factor results in high densities where population waves may develop. This assumption is justified by our interest in extinctions that often take place when high quality predators overexploit a region, giving rise to fatal population fluctuations.

2.7. Simulation experiments

In the experiments, the value of $Gain_{PD}$ and the number of walls and openings were varied; all other parameters were kept unchanged. Treatments consisted of an exhaustive combination of the values $Gain_{PD} = 10$ (baseline), 30, 50 and 70, combined with the complete set of wall-opening systems as represented in Fig. 1. (For each treatment, to avoid large fluctuation artifacts due to the initialization of individual population sizes, we implemented a delay of $t = 50$ in prey food re-growth and we discarded this data from

our analyses.) A large number (≥ 50) of simulation runs using different random seeds and $t = 10,000$ time steps were carried out for each treatment. Simulation results were obtained using a Dell T710 server under Ubuntu Linux and evaluated and graphed using the R statistical program package.

3. Results

As expected, the model populations behave in a qualitatively different fashion in the following 3 situations: unfragmented habitat, fragmented habitat, connected fragmented habitat (i.e., fragmented habitat with portals) (Figs. 1 and 2).

In the unfragmented habitat (Fig. 1A), both the prey and the predator populations tend to fluctuate heavily. After both prey and predator reach a peak, it is common for the prey population to collapse, especially at high values of $Gain_{PD}$ (high quality predator). Populations may coexist for long intervals, but the heavy fluctuations often drive the predator (or both) population extinct eventually (Fig. 3).

Habitat fragmentation (unconnected habitats) implies that the above dynamics occurs in many smaller areas independently (Fig. 1B). In some of these sub-habitats the predator goes extinct quickly (due to a suboptimal population mix at the starting time) and thus the prey will reach its maximum density in these sub-habitats. The short term extinction of predators is a typical and very important consequence of habitat fragmentation (Fig. 3). While these predator-free sub-habitats stabilize the fluctuation of the total number of prey, this stabilization is deceptive, because the sub-habitats that still contain predators continue to fluctuate wildly. Eventually the predators become extinct (especially, again, if $Gain_{PD}$ is large), because in the confined habitats the prey are easily overexploited. In many sub-habitats, only the prey food survives. The smaller the size of the sub-habitats in general, the faster the local (and henceforth global) extinction process (see also later).

Introducing passageways (openings) between the sub-habitats (Fig. 1C) have a profound effect. While the same local extinctions as described above tend to happen in these sub-habitats as well, yet sooner or later a repopulation of the prey can occur via the portals, followed by a delayed emergence of the predator. Fluctuations are generally more moderate (Fig. 3), because the prey can usually escape into a sub-habitat where there is plenty of food, but no predator. Predators are also more dispersed, compared to the sit-

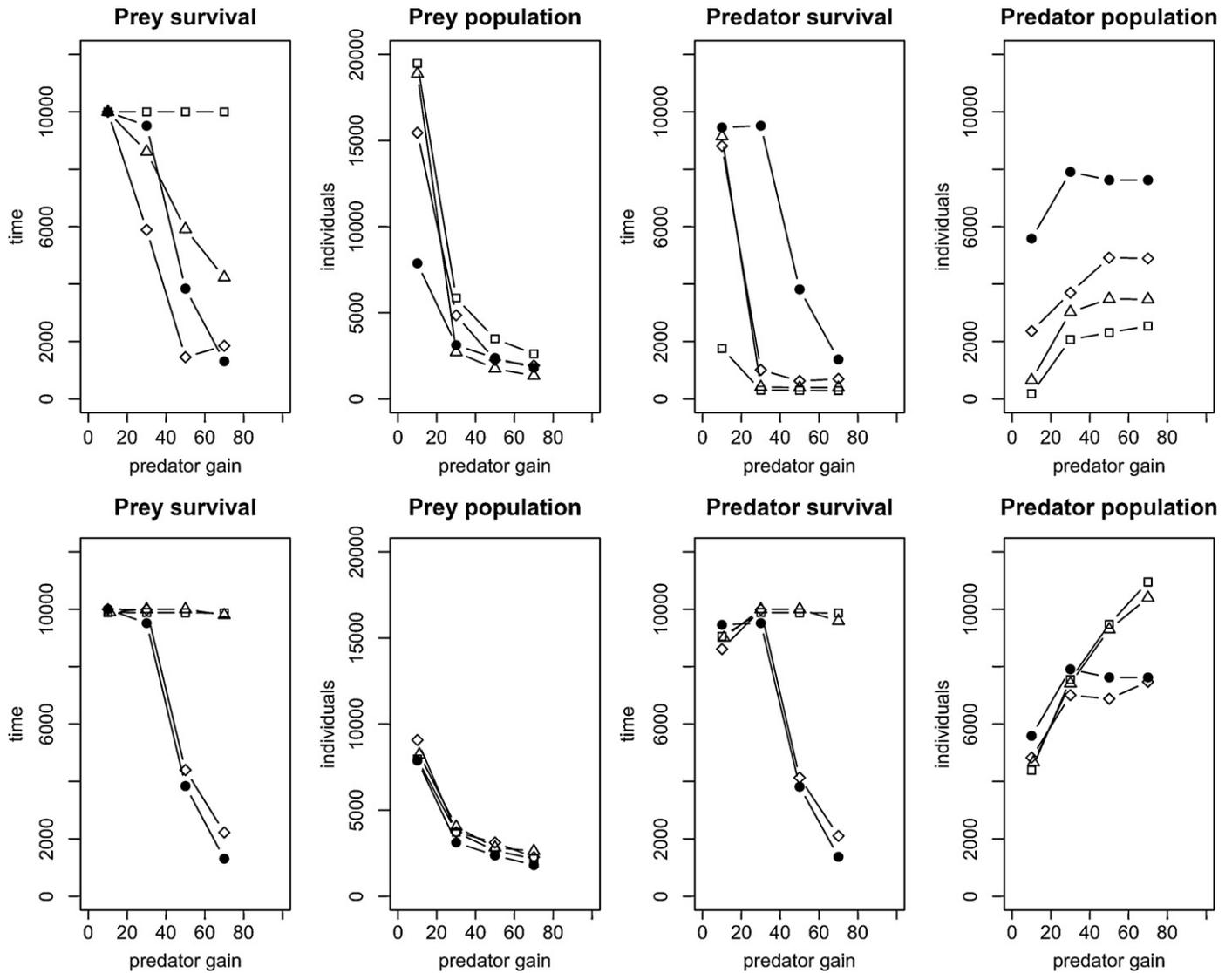


Fig. 4. Population size and survival time as a function of predator quality. *Upper row:* The effect of fragmentation without passageways. Full dot: $w0c0$; diamond: $w1c0$; triangle: $w2c0$; square: $w3c0$. *Lower row:* The effect of fragmentation with connectors. Full dot: $w0c0$; diamond: $w1c1$; triangle: $w2c2$; square: $w3c3$. The figure shows mean values for 50 different runs for each parameter value.

uations A and B, and therefore they are less prone to going extinct due to a concentrated overexploitation of the food resources.

In an unfragmented habitat, as $Gain_{PD}$ (the quality of the predator) increases, the prey population and its survival time declines, resulting in a usually small prey population also. This decrease of the prey population results in a decrease in the predator survival time if $Gain_{PD}$ is high ($Gain_{PD} > 30$). To understand the predator population's response, consider that when $Gain_{PD}$ is high, the predator decreases the prey population to a lower number. This also decreases the survival time of the prey, which in turn decreases the survival time of the predator again, so as a combined effect, the predator population remains near constant as a function of increasing $Gain_{PD}$ (Fig. 4, upper row).

Fragmentation drastically decreases the predator population size and survival time (Fig. 4, upper row). The increase of $Gain_{PD}$ has only a moderate effect now, rather, the predator population depends on how strongly fragmented the habitat is. On the other hand, prey survival and population size increase with the fragmentation. When fragmentation is introduced, it is easy to see that the sub-habitats start to play independent dynamics. The smaller the sub-habitats, the higher the chance that prey or predator go extinct.

Understandably, if the prey goes extinct first, then the predator follows shortly, while if the predator becomes extinct first, the prey will flourish in the given sub-habitat.

Implementing connectors (openings) between fragments results in a population boost for the predator, especially at high $Gain_{PD}$ and high fragmentation levels (Fig. 4, lower row). While the prey population decreases with $Gain_{PD}$ again, prey survival time radically increases when the habitat becomes more fragmented ($w \geq 2$).

This counter-intuitive result stems from the fact that the prey occasionally finds a temporal refuge, when it escapes through the portal to a neighboring sub-habitat that typically contains only food but no predators. The predator-free sub-habitats commonly emerge as the result of previous overexploitation of the prey, namely, in a small sub-habitat the predator can exterminate the prey and in turn the predator will starve and die off or leave the sub-habitat altogether. Because of the lack of prey, prey food will completely regenerate in the area, and the lack of predators will provide an ideal condition for the recolonization by the prey. The predators will at one point stumble upon the entrance points of these sub-habitats, but they can recolonize them only at a later

point when there is enough prey there. This delay allows the prey population to build up in population size. This not only gives the arriving predator plenty of food to eat, but some of the prey can colonize neighboring sub-habitats over and over again, thus repeating the process described above, before the predators can come in and start to prey upon them. This process in turn, ensures higher predator population size with higher survival times (Fig. 4, lower row).

Fragmented habitats with portals tend to decrease the oscillations of the populations (Fig. 5) and cut back on the variation of final population size as well as survival time (Fig. 6). In isolated fragmented habitats, fluctuations in the different sub-habitats are necessarily independent, and due to the restricted size of each sub-habitat, these fluctuations tend to be fast and with small amplitudes. In an unfragmented habitat, the fluctuations can be large and slow (promoted by medium values of $Gain_{PD}$). When $Gain_{PD}$ is high, the emergence of one or a few slowly moving spatial waves is frequently experienced (such waves are visible in Fig. 1A). The use of openings drastically changes the oscillation amplitudes, resulting in smaller phase volumes (Fig. 5). The phase volumes decrease with the number of sub-habitats and openings, but appear not to depend on the quality of the predator, if $Gain_{PD} \geq 30$. A further analysis of the frequency domain will be provided in Kamps and Karsai (in press).

Fragmentation always results in a substantial change, especially in the prey population and in the case of a high quality predator (Figs. 6 and 7). When the original habitat is fragmented into just a few sub-habitats (e.g., $w1$), the large variance in the survival time observed in the unfragmented case disappears and the resulting survival time becomes smaller for both prey and predator. More fragmentation ($w2$) not only increases the survival time of the prey, but also amplifies its variability, both in survival time and

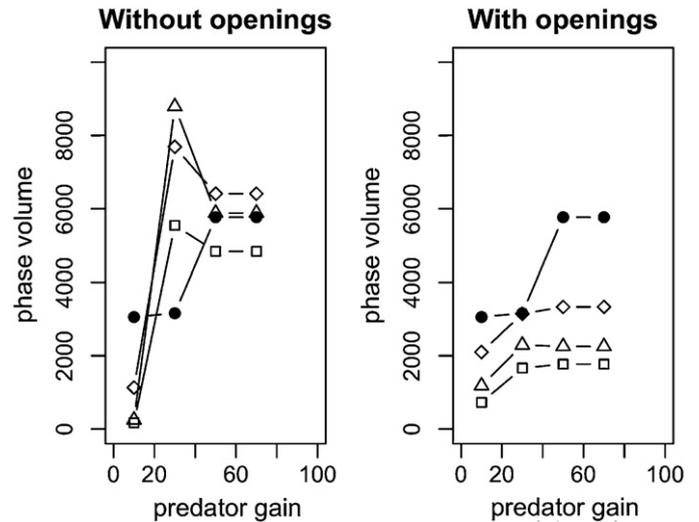


Fig. 5. Phase volumes with and without passageways. (A phase volume is defined here as the product of prey and predator population differences measured in a given time interval which is large enough to contain several periods.) Symbols are the same as in earlier graphs. Fragmentation without openings leaves oscillations largely unchanged, whereas the use of connectors radically decreases the oscillation amplitude.

numbers, due to the independent dynamics of the many isolated sub-habitats. However, this variability of the survival time disappears again, when even more fragmentation is introduced ($w3$) and thus the size of the prey population increases (Figs. 6 and 7, top graphs). The reason is that now predators commonly become extinct and the prey develops to saturation.

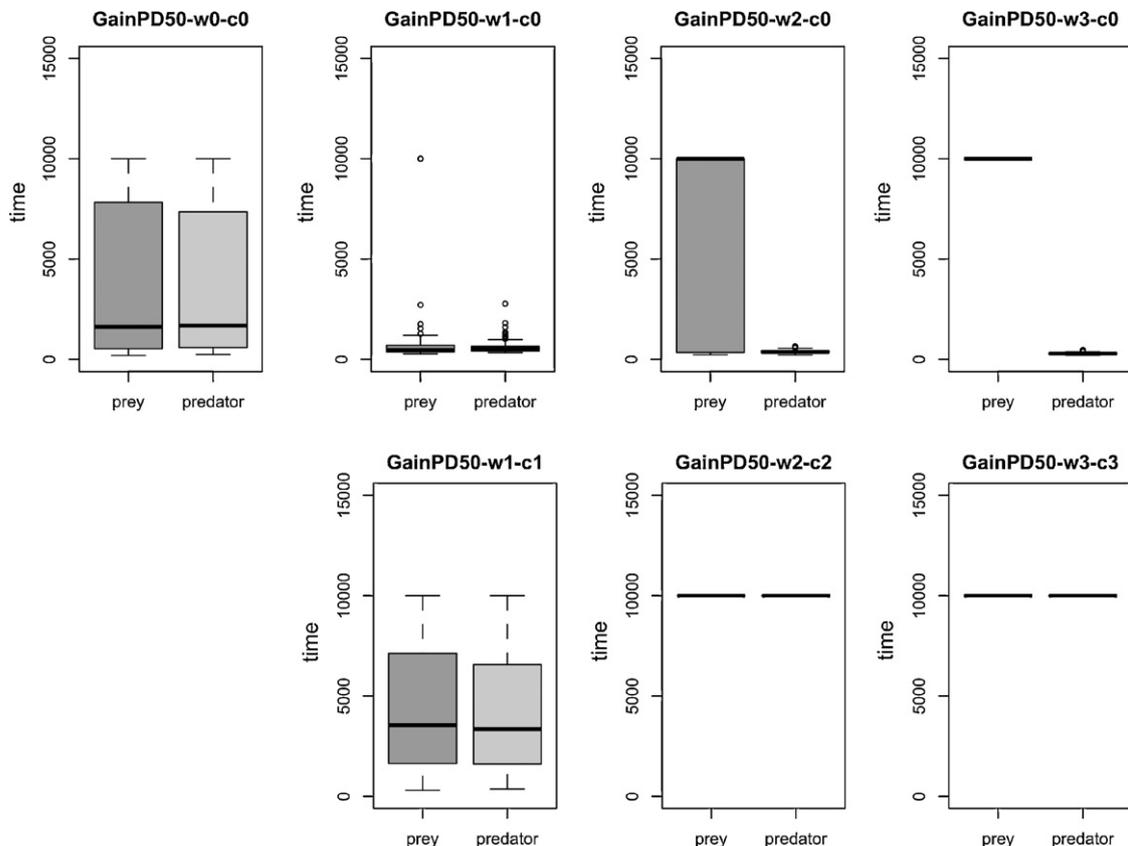


Fig. 6. Survival times for prey and predator with error bars in various fragmentation-opening systems using high quality predators ($Gain_{PD} = 50$). Upper row: No passageways (0–3 fragmentation borders in both the horizontal and the vertical direction). Lower row: Same arrangements but with openings between the fragments. Fragmentation, applied alone, decreases survival but fragmentation combined with openings increases survival beyond the unfragmented case.

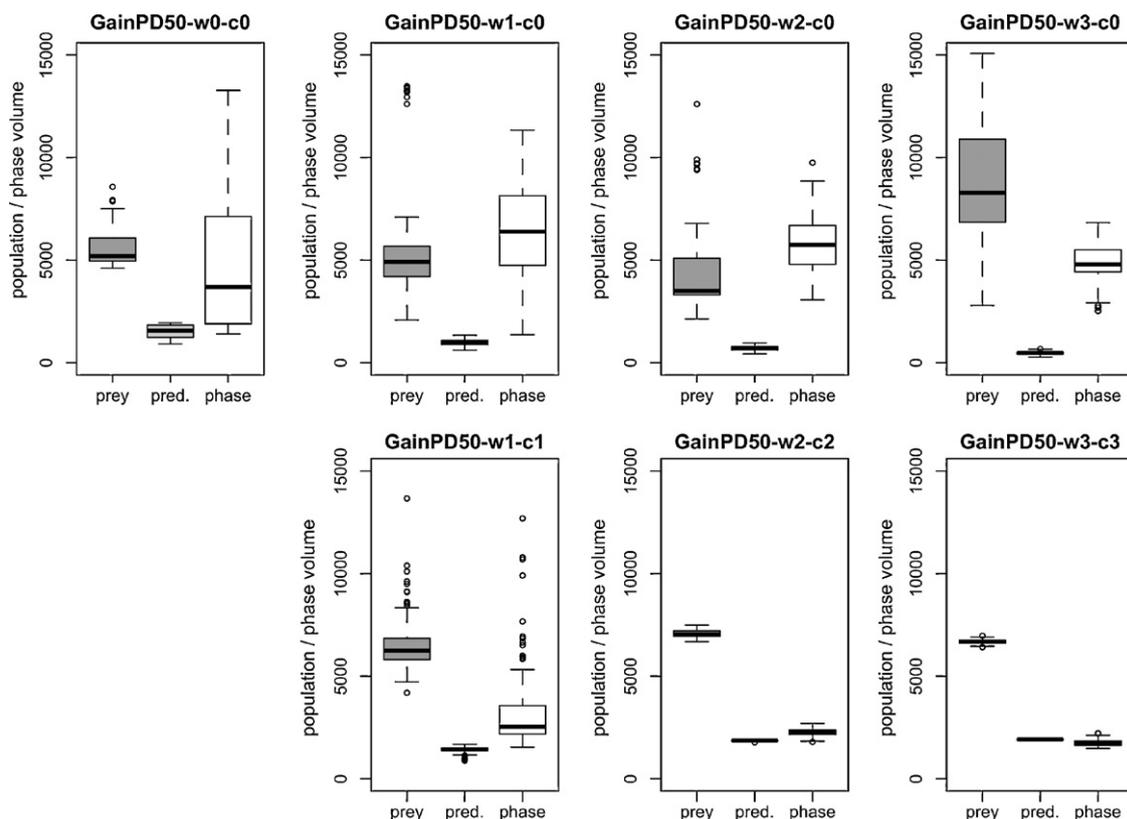


Fig. 7. Population numbers (normalized for unit energy) and oscillations (phase volumes) with error bars for prey and predator in various fragmentation–opening systems using high quality predators ($Gain_{pd} = 50$). Upper row: No passageways (0–3 fragmentation borders in horizontal and vertical direction). Lower row: Same arrangements but using openings between the fragments. Rightmost column shows phase volume. Fragmentation with passageways decreases oscillations; both fragmentation and the use of passageways decrease variation.

Connections between fragmented habitats increase the survival time and the population size of both the prey and the predator (Figs. 6 and 7, bottom graphs). The fragmented and connected habitats provide a more stable dynamics with smaller oscillations (i.e., phase volumes) and higher population sizes and increased survival times.

4. Discussion

We have studied a simple prey predator system in fragmented habitats where these habitats did not suffer a decrease in quality or overall size (i.e., habitat fragmentation without habitat loss). We have found fragmentation alone to be detrimental (in line with common expectation), but if combined with connecting portals to be even advantageous, by ensuring the coexistence of the prey and predator populations well above the level of the original unfragmented system.

Habitat fragmentation is conceptually commonly linked to habitat destruction and we believe that this may be the main reason for the controversial conclusions about the effect of habitat fragmentation on natural populations (Franklin et al., 2002). Doak et al. (1992) noted that very few studies have addressed the mechanisms by which fragmentation alone influences population dynamics. They suggested that an explicit consideration of spatial scale is essential in the discussions of habitat fragmentation and for devising effective conservation strategies. Our current study addressed both of these concerns. We found that fragmentation becomes detrimental for populations if resulting in small, isolated, disjoint sub-habitats. This was found especially true for the predator populations and for efficient predators that commonly drive the prey extinct before they themselves die out due to lack of food. While these dependen-

cies between the prey and predator are not new, our results point out that fragmentation even without destruction can endanger the predators of an area.

Our main finding, however, is counterintuitive and surprising. Connecting the fragmented sub-habitats with openings results in a very stable situation and ensures the coexistence of prey and predators with moderate fluctuations even for high quality predators and large population densities, at values where coexistence would not be granted even in a large undivided area. The scale seems to be important here as well. In the studied range, smaller fragments, if suitably connected, were more beneficial for the survival of the prey–predation system. The fragmented and connected sub-habitats provided a more stable dynamics with smaller oscillations and higher population sizes and survival times. In these environments, even very effective predators were able to flourish, because the fragmentation provided temporal refuges for the prey, therefore the predator was unable to globally overexploit and crash the prey population.

From the practical conservationist point of view, the earlier amalgamation of habitat loss and habitat fragmentation has made the evaluation of the roles of connectors such as wildlife corridors especially difficult. The debate about the effectiveness of corridors became one of the most important areas of debate for conservation, and as Simberloff et al. (1992) asserted, the lack of data necessitates a cautious approach, in order not to invest in constructing expensive corridors before we have quality information about their usefulness. Our study now shows that corridors (the connectedness of sub-habitats) indeed are essential to retain both the prey and the predator populations. Other factors such as the nature and required properties of the corridors, differences in sub-habitat quality and increased patchiness should be extensively studied in the future.

We want to discuss the issue of simplification in some detail. Our model has been stripped to what we believe to be the bare minimum of factors of highest generality to establish the case; as a consequence, the model does not directly address any given species and lacks several realistic details. For example, multi-species systems are characterized by several differences and tradeoffs. Varying migration speeds, movement patterns, switching between different prey types, the carrying capacity of the environment and the existence of different population interactions (competition, parasitism, symbiosis, etc.) may all modify the picture and require further studies in any given case – each case is subtly different. Also, different connection topologies and other spatial factors such as detailed geometry may alter the effects of migration. For example, simplifying the movement to pure random walk, and finding food and portals completely randomly seems unrealistic at the individual level. Nevertheless, from this simple setup a complex dynamic emerges in the model that includes a density dependent re-colonization of sub-habitats, delayed colonization by predators after the prey has colonized a sub-habitat, and so on. With the simplified model using as few different variables as possible we could more clearly concentrate on the effect of habitat fragmentation and connectedness on population size and survival. Thus we believe the presented model is suitable for grasping the “big picture” and clearly shows that habitat fragmentation can actually be beneficial for natural populations if accompanied by proper connections and not resulting in or paired with habitat destruction. The study also stresses that isolating the fragments is extremely harmful, and mainly so for the predator populations.

Experimental or observational data on natural populations largely agrees with the predictions of our simulations. Huffaker's (1958) experiment was one of the first to suggest that the subdivision of an available habitat into many smaller pieces (without habitat loss) can enhance the persistence of a predator–prey system. However, some consequences of his findings were not realized, until recent field and laboratory studies started to yield similar results (Spiller and Schoener, 1994; Gilbert et al., 1998; Holyoak and Lawler, 1996). For example, Kareiva (1987) found that increasing patchiness led to more frequent local explosions of aphid populations due to the effects of patchiness on the searching and aggregation behavior of ladybird predators. Our modeling result provides a support for these findings and predicts them to be quite general in nature.

These insights indicate that the conservation efforts need to consider the nature and behavior of the predator for planning passageways for effective connections. Dispersion among patches seems to be a key in the prey–predator system dynamics (Holyoak and Lawler, 1996) and this is an emergent dynamic variable in our simulation. Localizing corridors and moving through them is a consequence of a series of random events, but once it happens, the immigrants commonly find a quasi-ideal environment (with plenty of food) in the newly colonized sub-habitats. This yields a population explosion and the ensuing larger number of individuals has a better chance to stumble upon further corridors that can lead the population further, to new sub-habitats again. The emergent density dependence, paired with the restriction of dispersion due to fragment boundaries can produce a stabilizing effect on prey predator systems that can be utilized in conservation biology and helps understanding the dynamics of populations under natural conditions.

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