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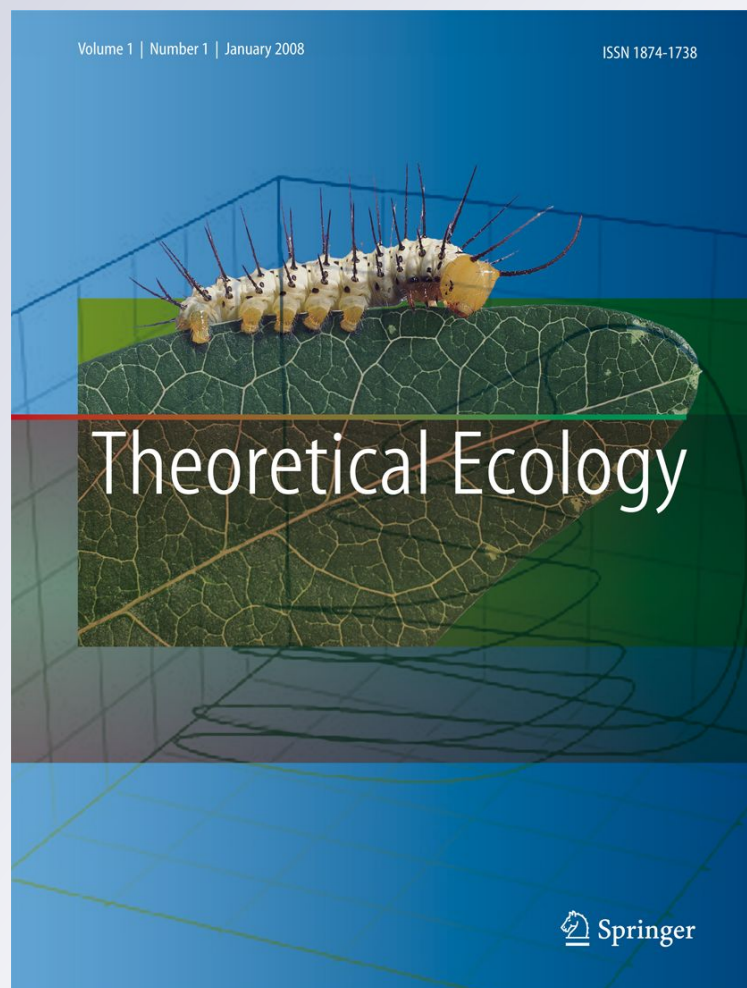
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Abstract We sought to understand how the separation of habitats into spatially isolated fragments influences the abundance of organisms. Using a simple, deterministic model of population growth, we compared analytically exact solutions predicting abundance of consumers in two isolated patches with abundance of consumers in a single large patch where the carrying capacity of the large patch is the sum of the carrying capacities of the isolated ones. For the deterministic model, the effect of fragmentation was to slow the rate of population growth in the fragmented habitat relative to the intact one. We also analyzed a stochastic version of the model to examine the effect of fragmentation on population abundance when resources vary randomly in time. For the stochastic model, the effect of fragmentation was to reduce population abundance.

We proved in closed-form, that for a non-equilibrium population exhibiting logistic population growth, fragmentation will reduce population size even when the total carrying capacity is not affected by fragmentation. We provide a theoretical basis for the prediction that habitat fragmentation amplifies the effect of habitat loss on the abundance of mobile organisms.

Keywords Habitat fragmentation · Logistic growth · Stochastic · Non-equilibrium · Model · Population

Introduction

Understanding why species vary in abundance and distribution has formed one of ecology's most enduring challenges (Soulé and Orians 2001), a challenge that has urgent relevance to contemporary environmental problems worldwide. Species are going extinct at rates that have been estimated to be 100–1,000 times more rapid than those that occurred for millennia and this rate is accelerating (Pimm et al. 1995, 2006). Unlike past large extinctions, the current loss of species is caused primarily by human activities, particularly modification of habitat (Pimm and Raven 2000; Pimm et al. 2006). These modifications result in habitat loss, degradation, and fragmentation, changes in landscapes that are believed to alter the trajectories of populations.

Revealing the consequences of human-caused and natural sources of fragmentation on the abundance of organisms has occupied theoretical and empirical workers for decades (Harrison and Bruna 1999; Haila 2002; McGarigal and Cushman 2002; Fahrig 2003; Tscharrntke and Brandl 2004; Ewers and Didham 2006; Fischer and Lindenmayer 2007; Stutchbury 2007), but conclusions

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of these studies are equivocal, with results that show positive, negative, and neutral effects (for review see Debinski and Holt 2000; McGarigal and Cushman 2002; Fahrig 2003). We believe this ambiguity arises because a variety of changes in landscapes have been lumped together as outcomes of fragmentation. These changes include shifts in area and quality of habitat, increases in patch isolation, and alteration of relationships between patch edge and interior (for review see Tscharrntke and Brandl 2004; Ewers and Didham 2006; Fletcher et al. 2007). Many of these effects are confounded. For example, as areas of suitable habitat become isolated from each other, total amount of habitat may decrease. This makes it difficult to disentangle the effect of changes in the area of habitat from effects of isolation. To avoid confusion in terms created by these confounding effects, we follow Fahrig (2003) and use fragmentation to mean the splitting of habitats into isolated parts, apart from any effect on habitat area or quality.

Here, we focus on a central, unresolved question: “Does habitat fragmentation influence the abundance of organisms in the absence of habitat loss?” We examine how habitat fragmentation influences the abundance of mobile organisms using simple deterministic and stochastic models. Our objective is to provide a theoretical basis for predicting how populations will respond to the isolating effects of fragmentation.

Our paper will be organized as follows. Firstly, we consider a simple system of differential equations to show that fragmentation will reduce the growth rate of populations that are not at equilibrium. We use this analytical result to explain patterns observed in discrete time simulations. We close by drawing biological conclusions about fragmented landscapes from our simulations and mathematical analysis.

Fragmentation in constant environments

We sought to create simple, general models allowing direct comparison of the total number of individuals in populations occupying multiple, small patches with a population occupying a single, intact habitat, where there are no differences in the area or the amount of resources between the intact habitat and the collection of the fragments. Moreover, we wanted to examine the effect of fragmentation on abundance when resources were temporally constant and temporally stochastic. To that end, we first used a deterministic, logistic model of population growth portraying dynamics of populations occupying two patches (representing the fragmented case) and a single patch (representing the unfragmented or intact, case). Carrying capacity was

initially treated as a time-invariant constant in these models, and the carrying capacity of the single patch was the sum of the carrying capacities of the fragmented patches. We compared analytically exact solutions of populations of the two patches with the population of the intact patch. In addition, we examined a stochastic version of the model to portray the effect of fragmentation on population abundance when resources vary stochastically in time.

Firstly, we explored the effect of fragmentation in an environment with temporally constant carrying capacity by examining the ordinary differential equation that describes logistic population growth:

$$\frac{dn(t)}{dt} = rn(t) \left[1 - \frac{n(t)}{k} \right], \quad t > 0, \\ n(0) = n_0. \quad (1)$$

Here, n is the number of individuals, k is the carrying capacity, and r is the per capita rate of growth in the absence of resource limitation, that is, when n is very small. (In general, we use lower case letters to denote deterministic quantities and capital letters to denote stochastic quantities.) Consider a population in an intact patch $n_{\text{intact}}(t)$ with carrying capacity k_{intact} . The patch is fragmented into two populations: $n_1(t)$ is the number of individuals occupying a patch with carrying capacity k_1 , and $n_2(t)$ is the number occupying a patch with carrying capacity k_2 . We specify that $k_{\text{intact}} = k_1 + k_2$. This is a simple way of representing the dissection of habitat without causing any change in habitat area or habitat quality—we simply assume that before fragmentation there is homogeneous use of resources by a thoroughly mixed population within the intact patch, but that after fragmentation resources are available to each population only within the patch it occupies.

Rates of change

We now show that dissecting the habitat reduces the total population size. The sum of rates of change of the two, fragmented, populations is given by

$$\frac{dn_1(t)}{dt} + \frac{dn_2(t)}{dt} \\ = rn_1(t) \left(1 - \frac{n_1(t)}{k_1} \right) + rn_2(t) \left(1 - \frac{n_2(t)}{k_2} \right) \\ = r \left[(n_1(t) + n_2(t)) - \left(\frac{n_1^2(t)}{k_1} + \frac{n_2^2(t)}{k_2} \right) \right], \quad t > 0. \quad (2)$$

Assume that a population becomes fragmented at a time $t = t^*$. In order to compare the rate of change

of an intact population with the sum of the rates of change in two fragmented populations at $t = t^*$, we let $n_{\text{intact}}(t^*) = n_1(t^*) + n_2(t^*)$. The rate of change of the intact population at the time of fragmentation is given by

$$\begin{aligned} \left. \frac{dn_{\text{intact}}(t)}{dt} \right|_{t=t^*} &= r(n_1(t^*) + n_2(t^*)) \left(1 - \frac{(n_1(t^*) + n_2(t^*))}{k_1 + k_2} \right) \\ &= r \left[(n_1(t^*) + n_2(t^*)) - \frac{(n_1(t^*) + n_2(t^*))^2}{k_1 + k_2} \right]. \end{aligned} \quad (3)$$

The difference between the sum of the rates of change of the patch populations and the rates of change of the intact population at the time of fragmentation is

$$\begin{aligned} \left. \frac{dn_1(t)}{dt} \right|_{t=t^*} + \left. \frac{dn_2(t)}{dt} \right|_{t=t^*} - \left. \frac{dn_{\text{intact}}(t)}{dt} \right|_{t=t^*} &= r \left[- \left(\frac{n_1^2(t^*)}{k_1} + \frac{n_2^2(t^*)}{k_2} \right) + \frac{(n_1(t^*) + n_2(t^*))^2}{k_1 + k_2} \right] \\ &= \frac{-r(n_1(t^*)k_2 - n_2(t^*)k_1)^2}{k_1k_2(k_1 + k_2)}, \end{aligned} \quad (4)$$

which is less than or equal to zero for all r, n_1, n_2, k_1 , and $k_2 > 0$, with equality when $\frac{n_1(t^*)}{n_2(t^*)} = \frac{k_1}{k_2}$, which obviously includes the case when $n_1(t^*) = k_1$ and $n_2(t^*) = k_2$, i.e., when both fragments and the intact population are at their equilibrium values. When the intact population is equal to the sum of the patch populations, the sum of the rates of change of the fragmented populations is always less than or equal to the rate of change of the intact population. We can conclude that for all subsequent times, $t > t^*$, the sum of the fragmented populations will be less than or equal to the intact population, because the fragmented population can only be-

come larger than the intact population by contradicting the inequality deduced from Eq. 4 at some later time. Ecologically, this means that fragmented populations grow more slowly to the combined carrying capacity than an intact population with the same total carrying capacity.

Explicit solutions

Alternatively, because the logistic growth differential equation can be solved explicitly for population abundance, we can directly compare the abundance in the intact habitat with the sum of the patch populations at any time, t . The solutions to the logistic initial value problems

$$\begin{aligned} \frac{dn_1(t)}{dt} &= rn_1(t) \left(1 - \frac{n_1(t)}{k_1} \right), \quad n_1(0) = n_{1,0}, \\ \frac{dn_2(t)}{dt} &= rn_2(t) \left(1 - \frac{n_2(t)}{k_2} \right), \quad n_2(0) = n_{2,0}, \\ \frac{dn_{\text{intact}}(t)}{dt} &= rn_{\text{intact}}(t) \left(1 - \frac{n_{\text{intact}}(t)}{k_{\text{intact}}} \right), \\ n_{\text{intact}}(0) &= n_{1,0} + n_{2,0}, \end{aligned} \quad (5)$$

are

$$\begin{aligned} n_1(t) &= \frac{k_1 n_{1,0} e^{rt}}{k_1 + n_{1,0}(e^{rt} - 1)}, \\ n_2(t) &= \frac{k_2 n_{2,0} e^{rt}}{k_2 + n_{2,0}(e^{rt} - 1)}, \\ n_{\text{intact}} &= \frac{(k_1 + k_2)(n_{1,0} + n_{2,0})e^{rt}}{(k_1 + k_2) + (n_{1,0} + n_{2,0})(e^{rt} - 1)}. \end{aligned} \quad (6)$$

In this constant environment model, the effect of fragmentation on abundance is

$$\begin{aligned} \Delta f(t) &= n_1(t) + n_2(t) - n_{\text{intact}}(t) \\ &= \frac{-e^{rt}(-k_1 n_{2,0} + k_2 n_{1,0})^2(e^{rt} - 1)}{[k_1 + n_{1,0}(e^{rt} - 1)][k_2 + n_{2,0}(e^{rt} - 1)][k_1 + k_2 + n_{1,0}(e^{rt} - 1) + n_{2,0}(e^{rt} - 1)]}, \end{aligned} \quad (7)$$

which is less than or equal to zero for all $t > 0$, with equality when either $\frac{n_{1,0}}{n_{2,0}} = \frac{k_1}{k_2}$ or when $t \rightarrow \infty$. This means that, in our constant carrying capacity model, when the population is not at equilibrium, the effect of fragmentation is to reduce the total population. When the fragmented and intact populations are at equilibrium, there is no difference between the sum of the patch populations and the intact population.

Multiple patches

Our result extends immediately to $I > 2$ patches. Let $m_I(t)$ be the population in a single intact environment with carrying capacity $\sum_{i=1}^I K_i$. We present the following inductive argument.

1. We have shown that $n_1(t) + n_2(t) \leq m_2(t)$
2. Assume $n_1(t) + n_2(t) + \dots + n_I(t) \leq m_I(t)$

3. Step #1 implies $m_I(t) + n_{I+1}(t) \leq m_{I+1}(t)$
 Step #2 implies $n_1(t) + n_2(t) + \dots + n_I(t) + n_{I+1}(t) \leq m_{I+1}(t)$

An identical argument can be applied to the rates of change.

Compounding fragmentation and habitat loss

The combined effect of fragmentation and habitat loss can be easily assessed as

$$n_{\text{intact}}(t) > n_{\text{intact,loss}}(t) \geq n_{1,\text{loss}}(t) + n_{2,\text{loss}}(t). \quad (8)$$

The inductive argument above allows us to extend this inequality to an arbitrary number of patches. This means that in this constant environment model, the population reduction due to both fragmentation and habitat loss is at least as large as that due to habitat loss alone and greater than that due to fragmentation alone.

Fragmentation in stochastic environments

Our initial model represents the unrealistic case that resources are fixed, resulting in a time invariant carrying capacity. This is particularly important because the results above suggest that population in the intact and fragmented habitat will be the same only when equilibrium is reached. Here, we add realism to our model by allowing carrying capacity to vary stochastically over time. In this model, we have chosen to view the intrinsic rate of increase, r , as a fixed parameter, and the carrying capacity, K , as a random variable. The intrinsic rate of increase represents the maximum growth rate when resources are not limiting and can be considered constant because it represents a characteristic of the species determined by its physiology and life history characteristics. In contrast, carrying capacity is not fixed, but instead varies in response to weather, disturbance, and other forces that we can assume to operate stochastically.

Effect of perturbations on rates of change

Firstly, consider the situation in which the population is at the mean carrying capacity and the carrying capacity increases, i.e., the situation when $n_1 = k$ and $k_1 = k + \epsilon$.

$$\begin{aligned} \frac{dn_1}{dt} &= rk \left(1 - \frac{k}{k + \epsilon} \right) \\ &= rk \left(\frac{k + \epsilon - k}{k + \epsilon} \right) \\ &= \frac{rk\epsilon}{k + \epsilon}. \end{aligned} \quad (9)$$

Secondly, consider the situation in which the population is at the mean carrying capacity and the carrying capacity decreases, i.e., the situation when $n_2 = k$ and $k_2 = k - \epsilon$. Then

$$\begin{aligned} \frac{dn_2}{dt} &= rk \left(1 - \frac{k}{k - \epsilon} \right) \\ &= rk \left(\frac{k - \epsilon - k}{k - \epsilon} \right) \\ &= \frac{-rk\epsilon}{k - \epsilon}. \end{aligned} \quad (10)$$

Notice that for all $\epsilon > 0$,

$$\left| \frac{dn_1}{dt} \right| < \left| \frac{dn_2}{dt} \right|,$$

and

$$\begin{aligned} \frac{dn_1}{dt} + \frac{dn_2}{dt} &= r \left[\frac{k\epsilon(k - \epsilon) + k\epsilon(k + \epsilon)}{(k + \epsilon)(k - \epsilon)} \right] \\ &= \frac{-2rk\epsilon^2}{k^2 - \epsilon^2} \\ &< 0, \end{aligned} \quad (11)$$

i.e., for a population at the deterministic equilibrium population $n = k$ and a change in carrying capacity of a given magnitude $|\epsilon|$, the population decreases when the carrying capacity is reduced at a faster rate than it increases when the carrying capacity is increased.

In particular, consider $\epsilon \sim \mathcal{N}(0, \sigma^2)$. Increases and decreases of carrying capacity of magnitude $|\epsilon|$ occur with equal probability, and we therefore expect that the long time average population will have $E[N] < K$.

Iterated map corresponding to solution via Euler's method

We begin a simple model to represent the effects of fragmentation in simulations, and later in analysis. We compare the predictions of two discrete logistic models, one representing a population occupying an intact landscape and the other portraying the population in two isolated fragments, where the sum of the resources in the two fragments is identical to the intact case. In both cases, we assume that the carrying capacity varies stochastically over time. Thus, our models portray fragmentation that occurs in the absence of habitat

loss in a temporally variable environment. Solving the logistic equation using Euler's method with a time step $\Delta t = 1$ results in the following iterated map for the intact case,

$$n(t+1) = n(t) + rn(t) \left(1 - \frac{n(t)}{k(t)}\right), \quad (12)$$

where $n(t)$ is the number of individuals at time t , r is the intrinsic rate of increase, and $k(t)$ is the carrying capacity at time t . Now imagine that the population is split into two fragments with no change in the overall carrying capacity. We represent this change as

$$n_1(t+1) = n_1(t) + rn_1(t) \left(1 - \frac{n_1(t)}{k_1(t)}\right), \quad (13)$$

$$n_2(t+1) = n_2(t) + rn_2(t) \left(1 - \frac{n_2(t)}{k_2(t)}\right). \quad (14)$$

Since we are using the Explicit Euler method to solve Eq. 1 for both the intact and fragmented cases, the inequality deduced from Eq. 4 is highly relevant. However, it is only valid provided $n_{\text{intact}}(t) = n_1(t) + n_2(t)$. If the intact and fragmented populations are equal at t^* , then using Eq. 4,

$$n_{\text{intact}}(t^* + 1) = n_1(t^* + 1) + n_2(t^* + 1) + \eta \quad \text{where}$$

$$\eta = \frac{(n_1(t^*)k_2 - k_1n_2(t^*))^2}{k_1k_2(k_1 + k_2)} r\Delta t. \quad (15)$$

It is possible to bound the time step so that $n_{\text{intact}}(t^* + 2) > n_1(t^* + 2) + n_2(t^* + 2)$, but in general, unlike the continuous case, when finding an approximate solution using Euler's method with a large enough time step, there is a potential for the sum of the fragmented populations to exceed the intact population at a given time step. However, in the limit of small time step when the ordinary differential equation system is solved accurately, the previous qualitative results obtained for the differential system apply.

We now consider the situation when the total carrying capacity is a stochastic quantity $K(t)$ with mean \bar{K} , i.e., where \bar{K} is the long-term average carrying capacity of the intact habitat. In a stochastic environment, the effect of the difference in growth rates between intact and fragmented population is exaggerated since the populations are generally far from equilibrium. We assumed that the intact habitat was divided into two fragments with carrying long-term average carrying

capacities $\bar{K}_1 = p\bar{K}$ and $\bar{K}_2 = (1-p)\bar{K}$, $0 < p < 1$. Equations 12, 13 and 14 become

$$N(t+1) = N(t) + rN(t) \left(1 - \frac{N(t)}{K(t)}\right), \quad (16)$$

and

$$N_1(t+1) = N_1(t) + rN_1(t) \left(1 - \frac{N_1(t)}{K_1(t)}\right), \quad (17)$$

$$N_2(t+1) = N_2(t) + rN_2(t) \left(1 - \frac{N_2(t)}{K_2(t)}\right), \quad (18)$$

where $K(t) = K_1(t) + K_2(t)$ at all times t . We used Eqs. 16 and 17, 18 to simulate the effects of fragmentation on average abundance, on the average rate of population increase for populations above and below \bar{K} , and on the average distance of the populations from \bar{K} . We examined how the magnitude of the effect of fragmentation depended on the (temporal) variance in $K(t)$, the correlation between $K_1(t)$ and $K_2(t)$, and variation in r . Simulations were conducted by drawing random values of $K_1(t)$ and $K_2(t)$ at each t from a multivariate normal distribution with means $p\bar{K}$ and $(1-p)\bar{K}$, respectively, and specified variance and covariance, and setting $K(t) = K_1(t) + K_2(t)$. Initial conditions for each population were defined to be $N_1(0) = p\bar{K}$, $N_2(0) = (1-p)\bar{K}$ and $N(0) = \bar{K}$.

Because we wanted to isolate the effects of fragmentation apart from effects mediated by extinction risk, we prevented population extinctions by constraining the minimum population size to 1. Five hundred replicate simulations were run for 100 time steps and the steps 1–25 were discarded from each replicate to remove possible transients. We examined how the magnitude of the effect of fragmentation depended on temporal variance in $K(t)$, correlation in $K(t)$ between fragments, variation in r and variation in K .

Simulations revealed that the average size of the population in the intact habitat exceeded the average of the sum of the two fragments for all cases considered (Fig. 1), and that the average rate of increase of the intact population was greater than the average rate of increase of the sum of the fragmented population whenever $\bar{N}_i(t) < \bar{K}_i$ (Fig. 2), that the average rate of decline of the sum of the fragmented population exceeded the average rate of decline of the intact population whenever $\bar{N}_i(t) > \bar{K}_i$ (Fig. 2). The magnitude of the effect of fragmentation increased with increasing values of r (Fig. 1a), increased with increasing variance in K (Fig. 1c), and decreased with increasing correlation in

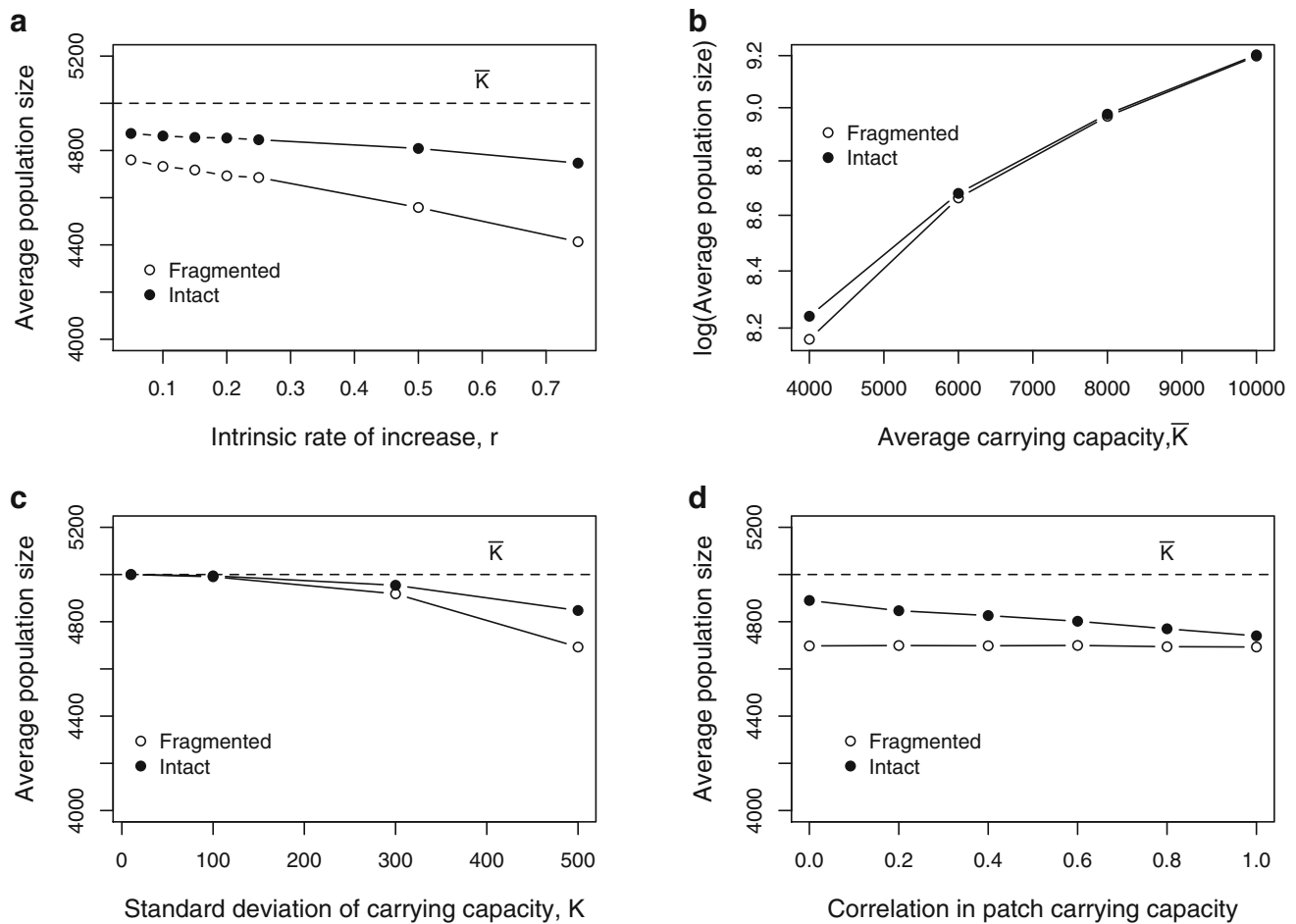


Fig. 1 Simulations of the responses of the long term average population size to habitat fragmentation. Each point is the mean of 500 replicates of a 100 step time series, from which the first 25 steps were excluded to minimize the influence of the choice of initial conditions. Populations were not allowed to go extinct by constraining the population size to be ≥ 1 in each replicate time series. For all plots $p = 0.6$. Unless otherwise stated, the parameter values in plots (a–d) were $r = 0.2$, $\bar{K} = 5,000$, stan-

dard deviation of $K = 500$, correlation in K between fragments = 0.25. **a** Increasing the intrinsic rate of increase r amplified the effect of fragmentation on \bar{N} . **b** Increasing the average carrying capacity \bar{K} attenuated the effect of fragmentation. **c** Increasing the temporal variance in K increased the effect of fragmentation. **d** Increasing the correlation between the fragment carrying capacities decreased the effect of fragmentation

carrying capacities of the fragments (Fig. 1d). Qualitatively, these results were robust to a broad range of choices of parameter values.

Discussion

In our study, we asked the question: “Does habitat fragmentation influence the abundance of organisms in the absence of habitat loss?”. We examined how habitat fragmentation affects the abundance of mobile organisms in constant and randomly varying environments by using simple deterministic and stochastic models. Our objective was to provide a theoretical prediction

for how populations respond to the isolating effects of fragmentation in the absence of habitat loss.

Using a deterministic, logistic model in continuous time, we show analytically that the sum of the growth rates of fragmented populations is less than or equal to the growth rate of an intact population with a carrying capacity equal to the sum of the carrying capacities of the fragmented populations. Growth rates are equal only when the populations are at equilibrium (when $n_1(t) = k_1$, $n_2(t) = k_2$) or when the ratio $\frac{n_1(t)}{n_2(t)} = \frac{k_1}{k_2}$.

These conditions are unlikely to be met in nature because we expect the resources that support populations to vary over time, and if that variation is sufficiently large, populations may never equilibrate (Wiens 1977;

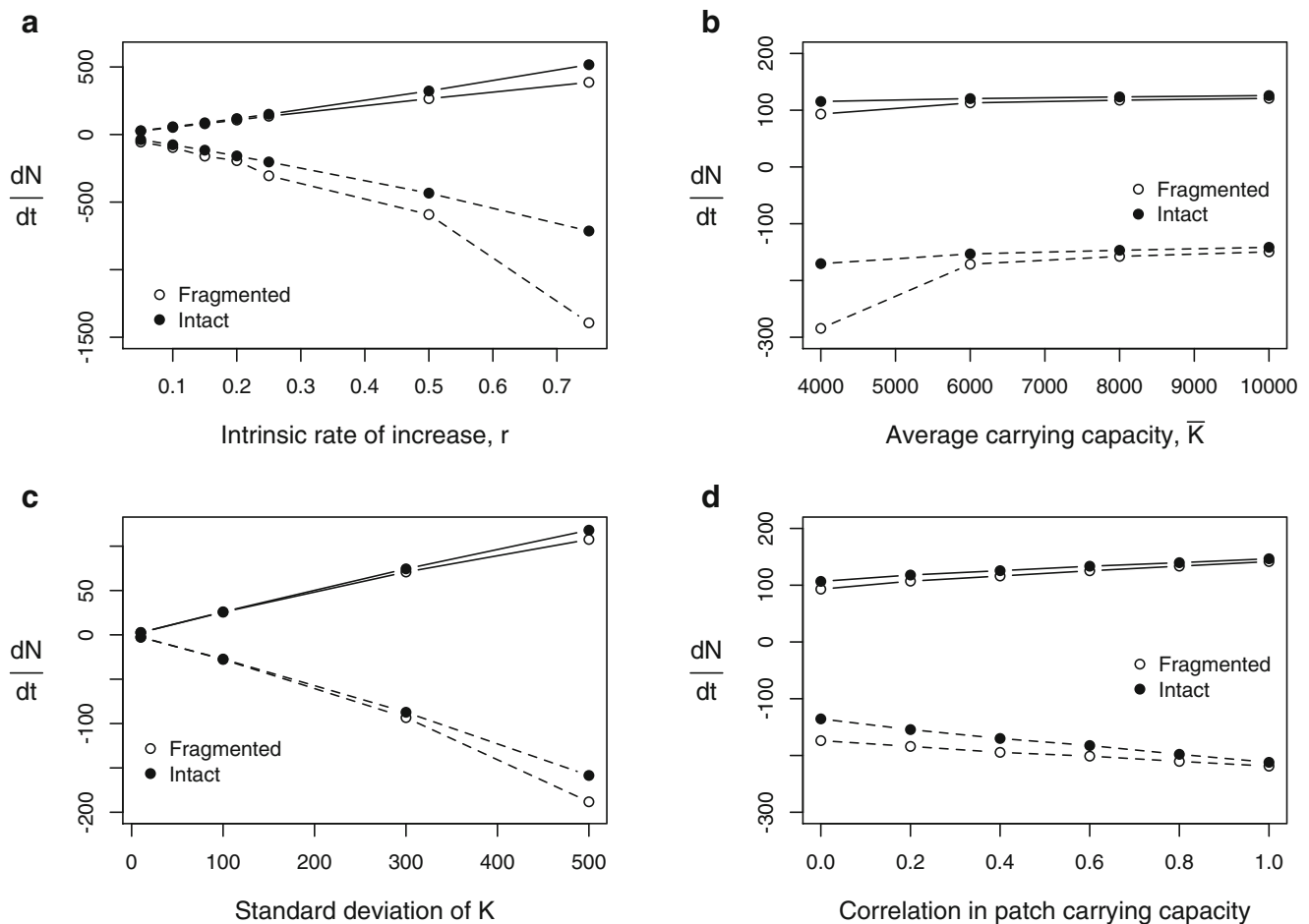


Fig. 2 Stochastic simulations of the responses of the population growth rate to habitat fragmentation. Each point is the mean of 500 replicates of a 100 step time series, from which the first 25 steps were excluded to minimize the influence of the choice of initial conditions. Populations were not allowed to go extinct by constraining the population size to be ≥ 1 in each replicate time series. For all plots $p = 0.6$. Unless otherwise stated, the parameter values in plots (a–d) were $r = 0.2$, $\bar{K} = 5,000$, standard deviation of $K = 500$, correlation in K between fragments = 0.25.

a Increasing the intrinsic rate of increase r amplified differences in $\frac{dN}{dt}$ between fragmented and intact populations both above (solid line) and below carrying capacity. **b** Increasing the average carrying capacity \bar{K} attenuated the effect of fragmentation. **c** Increasing the temporal variance in K increased the effect of fragmentation on population growth rate. **d** Increasing the correlation between the fragment carrying capacities decreased the effect of fragmentation

Ellis and Swift 1998; Smith 2010). It is reasonable to expect that the magnitude, if not the direction, of the effect of fragmentation will depend upon the values of parameters regulating population growth and upon the nature of the temporal variation in K . To explore this dependence, we conducted discrete time simulations. These simulations revealed that the effects of fragmentation will be greatest when the temporal variation in carrying capacity is largest (Fig. 1c), when the intrinsic growth rate of the population is large relative to the carrying capacity Fig. 1a), and when the carrying capacities of fragments are weakly correlated in time (Fig. 1d). Fragmentation-induced differences in population growth rate mediated these differences in

average abundance; large effects on average abundance corresponded to large effects on growth rates (Fig. 2).

These results are biologically sensible. The average fragmented population will be smaller than the average intact one because the rate of decline of the fragmented population above \bar{K} is greater than, and the rate of increase below \bar{K} is less than, the corresponding rates of the intact population (Fig. 2). The magnitude of this difference depends on $\frac{r}{\bar{K}}$. When r is small relative to \bar{K} , departures of population size from the long-term equilibrium will be smaller than when r is large relative to \bar{K} because the strength of density dependent feedback to per-capita population growth is weaker when $\frac{r}{\bar{K}}$ is small (Fig. 1a, b). When $\frac{r}{\bar{K}}$ is large, stochastic departures

from \bar{K} are correspondingly large, magnifying the effect of population growth rate on average population size by amplifying the potential for the population to overshoot carrying capacity. Increasing correlation in K between patches compresses the effect of fragmentation perhaps because covariation in carrying capacity of habitat fragments increases the probability that $\frac{N_1(t)}{N_2(t)} = \frac{K_1(t)}{K_2(t)}$. All of these effects extend logically from our analytical results.

Others have contributed theory relevant to our objective. Freedman and Waltman (1977) and Holt (1985) examined equilibrium population abundance with two-patch, temporally constant carrying capacity models. Freedman and Waltman (1977) compared equilibrium populations between two-patch models with a variable rate of dispersal between the two patches. Freedman and Waltman's two-patch model, using logistic density dependence, is described by

$$\begin{aligned}\frac{dn_1(t)}{dt} &= r_1 n_1(t) \left[1 - \frac{n_1(t)}{k_1} \right] - \epsilon n_1(t) + \epsilon n_2(t) \\ \frac{dn_2(t)}{dt} &= r_2 n_2(t) \left[1 - \frac{n_2(t)}{k_2} \right] - \epsilon n_2(t) + \epsilon n_1(t)\end{aligned}$$

where r_1 and r_2 are the patch intrinsic growth rates. The two patches are separated by a barrier whose strength is inversely proportional to ϵ . The case of $\epsilon = 0$ corresponds to isolated patches, and it is proposed that the limit as ϵ approaches infinity corresponds to complete and unrestricted mixing between patches. In this model, Freedman and Waltman (1977) show that “isolated” patches ($\epsilon = 0$), can maintain a larger population than fully mixed patches. Holt (1985) extended Freedman and Waltman's model, allowing different patch growth rates as well as different, though constant, patch carrying capacities. Holt (1985) found that total equilibrium populations for isolated patches may have either greater or smaller populations than in patches with infinite dispersal, depending on the relative values of patch growth rates and carrying capacities. Underwood (2004) extended Freedman and Waltman's model by simulating patch populations with randomly varying patch carrying capacities and growth rates. These simulations also showed that average populations in isolated patches could be larger or smaller than in patches with dispersal, depending on the amount of variation in, and correlation between, patch growth rates and carrying capacities. However, when patch carrying capacities varied while patch growth rates were held constant, Underwood's simulations showed average patch populations with dispersal were smaller than patch populations without dispersal, revealing the

same relationship as the time-constant environment Freedman and Waltman (1977) model. That is, the sum of completely isolated patch populations was greater than the population when dispersal between patches was allowed.

We contrast this with our results for our stochastic model where fragmentation always resulted in a reduction in the long-term average of the population. To see where our model differs from Freedman and Waltman (1977), and subsequent papers it is useful to re-scale Freedman and Waltman's (1977) model with $\tau = \epsilon t$. Freedman and Waltman's Eq. 3.1 then becomes

$$\begin{aligned}\frac{dn_1(\tau)}{d\tau} &= \frac{r_1}{\epsilon} n_1(\tau) \left[1 - \frac{n_1(\tau)}{k_1} \right] - n_1(\tau) + n_2(\tau) \\ \frac{dn_2(\tau)}{d\tau} &= \frac{r_2}{\epsilon} n_2(\tau) \left[1 - \frac{n_2(\tau)}{k_2} \right] - n_2(\tau) + n_1(\tau)\end{aligned}$$

The re-scaling demonstrates that as $\epsilon \rightarrow \infty$ and dispersal increases such that in the limiting case there is no barrier to migration, the first term in each equation approaches zero and the rates of change of the patch populations become essentially *independent* of the patch carrying capacities and intrinsic growth rates. In the limit as $\epsilon \rightarrow \infty$, the model reduces to a mass-balance equation whose (periodic) solution depends entirely on the initial patch population conditions and is independent of r_i and k_i . Biological information for the organism's characteristics and life history that is embedded in r_i and k_i has been lost. Freedman and Waltman's model and our model are useful for addressing different ecological situations. Freedman and Waltman's model is useful when dispersal is limited, that is, there is some intermediate level of dispersal between patches, and biological information is maintained. However, we argue that the Freedman and Waltman's model is not useful for describing the “intact” case when there is unlimited dispersal amongst patches. In our model, the biological information contained in r and k is maintained when we compare the sum of isolated populations with an intact population with the same total carrying capacity.

Our results depend on the assumption that habitats become fragmented more rapidly than the characteristic time scale of population growth. We do not find this assumption confining—in nature, fragmentation often occurs quickly—fences dissect landscapes, roads appear suddenly, landscapes are converted from one type to another (reviewed by Galvin et al. 2008; Hobbs et al. 2008). However, there will be cases where fragmentation occurs gradually and in these cases, populations with rapid population growth may not see the effects we have shown here.

Our findings are relevant to species conservation by providing a general, predictive theory for the effects of habitat fragmentation apart from the effects of habitat loss. Although idiosyncrasies in life histories may cause the loss of habitat to affect different species in somewhat different ways, particularly over the short term, the general effect is quite predictable—if the area of habitat declines dramatically, so will the abundance of a species that requires that habitat. However, a theory of the effects of habitat fragmentation, which we define as the isolation of populations independent of habitat loss, has been slow to emerge. We show that fragmentation will reduce population abundance even when the total amount and quality of habitat remains unchanged. There is emerging empirical support for this prediction (Blackburn et al. 2010; Searle et al. 2010).

Our work suggests that additional simulation studies may be fruitful. We have run preliminary simulations with the deterministic theta-logistic population growth model where $\theta \neq 1$ (Sibly et al. 2005). These initial simulations showed the same results as for our logistic population growth: the intact population is greater than that of the total fragmented population when the populations are not at equilibrium. For biologically meaningful parameters ($r > 0, k > 0$), an analytical, real-value solution to the theta-logistic population equation is not known. A complete computational exploration for the theta-logistic model comparing intact and fragmented populations is beyond the scope of this study, but may provide insight into more general population growth models.

Conclusions

We examined how habitat fragmentation influences the abundance of mobile organisms using simple constant environment and randomly varying environment models. In our constant environment model, fragmentation results in a reduction in population whenever the population is not at equilibrium. In our randomly fluctuating model, fragmentation leads to a decrease in the expected population, and this decrease becomes larger as the intrinsic growth rate increases (Fig. 1a) and as the variance of the carrying capacity increases (Fig. 1c). As intrinsic growth rate decreases, a population is less able to respond quickly to changes in amount of resources. The effects of this inability are amplified by increasing the magnitude of the temporally random variation in resources. For intact populations in a “bad year” the entire population is reduced. However in a “good year”, the entire population benefits while the population in an isolated patch is unable to utilize excess resources

that exist in another patch. The net effect is that intact environments support higher average populations.

The precise circumstances examined here may not occur even when landscapes are dissected by roads or fences with nominal reductions in habitat area, since habitat quality may change (for review see Trombulak and Frissell 2000; Hayward and Kerley 2009). We do not attempt to account for the many, detailed influences that may alter the relationship between habitat area and population density (for reviews see Connor et al. 2000; Gaston and Matter 2002). It is clear that if the area of habitat available to a population declines sufficiently, that the number of individuals in a population must decline. Because habitat fragmentation is often accompanied by habitat loss, our results might appear to be idiosyncratic. However, our findings are general because they provide a theoretical basis for the effects of habitat fragmentation resulting from isolation acting alone, effects that can be reasonably expected to add to the effect of habitat loss.

We provide a theoretical basis to focus future research on habitat fragmentation. In systems where the effect of habitat loss is distinct from habitat fragmentation, our results present the clear, testable hypothesis that the abundance of intact populations is larger than the abundance of fragmented populations even when the total amount of resources is equal. In addition, our model motivates the hypothesis that fragmentation adds to the population reduction associated with habitat loss. This work readily lends itself to experimental studies.

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