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The process of connectivity loss during habitat fragmentation and their consequences on population dynamics



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ABSTRACT

Understanding the processes and consequences of habitat fragmentation is highly relevant since it represents a serious threat to biodiversity. However, fragmentation includes several facets that are difficult to dissect, such as loss of habitat connectivity, edge effects, and habitat loss. In this study, we analyze by mathematical and computational means a single isolated component of habitat fragmentation: the loss of connectivity. The main novelty of our approach is that we consider the entire temporal process by which a continuous habitat gets progressively divided into two isolated patches. For this purpose, we present a new mathematical model. Our results indicate that, in line with empirical evidence, connectivity loss derived from habitat fragmentation could lead to either a decrease or an increase in total population abundance during the process. We give some conditions under which the mentioned effects should occur. We conclude that connectivity loss could exert strong influences on non-equilibrium populations.

1. Introduction

Biodiversity is being currently depleted at unprecedented rates (Cardinale et al., 2012; Butchart et al., 2010). One of the main causes of such crisis is the fragmentation of habitat (Wu, 2013), that consists of the division of a continuous habitat into smaller isolated pieces of habitat immersed into a matrix of human-disturbed land. Fragmentation accounts for up to 75% biodiversity loss, concurrent with a severe depletion of ecosystem services (Haddad et al., 2015).

Habitat fragmentation is not a simple phenomenon. At least, there are three main sources of disturbance generated by such a process: (1) loss of connectivity, (2) habitat loss, and (3) edge effect. Connectivity loss (or fragmentation *per se* Fahrig, 2003) is understood as a process in which a single, large patch is subjected to one or several divisions within it that leads to the formation of several smaller disconnected patches. The geographical isolation of the remaining habitat impedes that certain species migrate between patches. Habitat loss results from the replacement of original, suitable habitat into matrix, hostile to most native species, in which the fragments get immersed. Total area, summed over all patches, get smaller than original area. Edge effect results from increasing the length of border as a consequence of habitat division. Borders constitute the contact zone with the matrix, and survival of species often decrease there because of an increased occupation

of the matrix and because of increased antagonistic species interactions with natural enemies. The relative contribution of each of the component factor to the total adverse effect reported for the fragmentation complex remains controversial. However, available evidence suggests that edge effect and habitat loss exert the largest effects and that the consequences of connectivity loss could be of minimal impact, and indeed could also enhance population abundance (Fahrig, 2003).

As stressed in Fahrig (2003), our understanding of the population consequences of habitat fragmentation has been hampered by the lack of distinction between the components of the fragmentation process. Besides this, most previous analytical studies have studied habitat fragmentation through comparing two static states: continuous versus fragmented habitat, and have not dealt with this phenomenon as a genuine process. In the course of this process, connectivity loss progressively limits species dispersal, shaping population dynamics prior to complete isolation of remnant patches (see Fig. 1).

In this study we isolate a single factor within the fragmentation phenomenon: habitat connectivity loss, to analyze its consequences on single-species population dynamics. Moreover, and unlike previous work, we address the continuous nature of the fragmentation process. For this, we present and analyze mathematically a single-species population dynamics model that covers the whole succession of system states (from a to c in Fig. 1), in contrast to prior models that usually

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Fig. 1. Three snapshots of the fragmentation process through time, occurring on the habitat Ω : (a) state of the habitat before the beginning of the fragmentation process, $\Omega(t)$ composed of subregions *A*, *B* and a shared border Γ ; (b) state of Ω in a time just after the initiation of the fragmentation process, where Γ has lost a part $\Gamma(t)$ of border, and (c) habitat state after the fragmentation process was finished, where $\Omega(t)$ is the union of disjoint fragments *A* and *B*, and the shared border Γ has disappeared.

compare states **a** versus state **c** only, disregarding the population dynamics driven by the processes occurring *during* fragmentation. Our aim is to understand under which circumstances if any, connectivity loss by itself drives either transient or long-term changes in population abundances.

The rest of this paper is organized as follows: In the next section, we present our model step by step, ending with the general equations which represent the rates of changes in abundance when a population is being subjected to a loss of connectivity between two subregions. Then, we present the main results of a mathematical analysis of our model. Next, we show numerical results to show the model behavior in a population simultaneously subjected to habitat fragmentation and an independent periodic perturbation. We end this paper with a discussion of our results.

2. The model

We will assume a deterministic and continuous-time dynamics. If the population is located in a habitat represented by a set $\Omega(t)$ of the space at time $t \ge 0$ whose measure (e.g. area) is given by $m(\cdot)$, and the population abundance is denoted by x(t), then the population growth rate is governed by the differential equation

$$x'(t) = x(t)r[D_{\Omega(t)}], \tag{1}$$

where $r[\cdot]$ is the time-varying per capita growth rate as a function of population *density* $D_{\Omega(t)}$, given by the population abundance per unit area, *i.e.*, $D_{\Omega(t)} = x(t)/m(\Omega(t))$. There is sufficient evidence of density-dependent negative feedback (see Hixon et al., 2002; Sinclair, 1989; Tanner, 1966), so that we will assume $r[\cdot]$ being a decreasing function.

If A(t) is a subset of $\Omega(t)$ and $B(t) = \Omega(t) \setminus A(t)$ is its complement, then the total population abundance is equal to the sum of the abundances in each subset, that is, $x_{A(t)} + x_{B(t)}$. This equality expressed in terms of the growth rates is

$$x' = x'_{A(t)} + x'_{B(t)} = x_{A(t)} r [D_{A(t)}] + x_{B(t)} r [D_{B(t)}].$$
(2)

If $D_{A(\cdot)}$ and $D_{B(\cdot)}$ are assumed to be equal to $D_{\Omega(\cdot)}$, then eqn. (2) reduces to eqn. (1).

On a time interval [0, T], T > 0, let us assume that a population is being subjected to the process of fragmentation during a subinterval $[t_i, t_f]$, $0 < t_i < t_f < T$. This population is located in a habitat represented in mathematical terms by a region (an open, connected, bounded and non-empty set) Ω of \mathbb{R}^2 . To represent the division of a continuous habitat into two isolated patches by the development of a discontinuity, we assume that Ω is the union of three disjoint sets: two regions *A* and *B*, and a common frontier $\Gamma \subset \partial A \cap \partial B$ (sign ∂ indicates the boundary of), which is an arcwise connected set. Moreover, we assume that Γ is the graph of a regular and simple curve α : $(t_i, t_f) \to \Omega$ such that $\alpha(t_i^+)$ and $\alpha(t_f^-)$ exist in $\mathbb{R}^2 \backslash \Omega$.

Writing $\Gamma(t) = \{\alpha(s): s \in (t_i, t_f)\}$ with $t \in (t_i, t_f)$, we have that, at any moment *t* of the process, the habitat is represented by the set $\Omega(t) = \Omega \setminus \Gamma(t)$. Note that we have a *continuous habitat*, *i.e.*, $\Omega(t) = \Omega$ for $t \leq t_i$ because $\Gamma(t_i^+) = \phi$, and a *fragmented habitat*, *i.e.*, $\Omega(t) = A \cup B$ for $t \geq t_f$ because $\Gamma(t_f^-) = \Gamma$. Then, at $t \leq t_i$ the population is in a unique patch Ω , but after the final instant, $t \geq t_f$, the population is distributed over two isolated patches *A* and *B*, see Fig. 1. Note that the loss of habitat at time $t \in (t_i, t_f)$ is $\Gamma(t)$, a set of measure (area) zero. Therefore, our model considers only the loss of connectivity without habitat loss and without decreased habitat quality (e.g. expressed as edge effect).

Our interest is to develop a unified model equation for the population dynamics before, during, and after the fragmentation process, which constitute the main novelty of this modeling exercise. Now we present equations for each of the major phases involved in the fragmentation process, and then the general model for the entire process.

Continuous habitat $(0 \le t \le t_i)$: In this time interval, the subregions *A* and *B* are only a conceptual division of Ω and are fully connected, see Fig. 1a. If we assume that areas of measure zero never contain any individuals, then the total population growth rate is

$$(x_A + x_B)' = (x_A + x_B) r [D_\Omega], \quad t \in [0, t_i],$$
(3)

which is another form of Eq. (1).

Fragmented habitat ($t_f \le t \le T$): In this time interval, the zones *A* and *B* are physically divided by Γ and isolated from each other to the migration of population members. So, they form two disjoint patches, see Fig. 1c. Nevertheless, there has been no loss of habitat in the process because $m(\Gamma) = 0$. Then we have two decoupled ordinary differential equations governing the growth, one for each patch. That is,

$$\begin{cases} x'_{A} = x_{A}r[D_{A}], \\ x'_{B} = x_{B}r[D_{B}], \end{cases} t \in [t_{f}, T]. \end{cases}$$
(4)

Transitional phase $(t_i < t < t_f)$: To model the population growth rate during the whole process of habitat fragmentation (see Fig. 1b), we present the following differential system:

$$\begin{cases} x'_A = x_A r \left[D_{A \cup B(t)} \right] \\ x'_B = x_B r \left[D_{A(t) \cup B} \right] \end{cases} \quad t \in (t_i, t_f),$$
(5)

where $A \cup B(t)$ (and $A(t) \cup B$) is an extension of the zone A (and B) in a subset B(t) of B (and A(t) of A). To calculate the population density at A, B(t) represents the area of influence of the demographic type of Bat the instant t. The same for B(t) respect to A. Note that $A(\cdot)$ and $B(\cdot)$ are functions from [0, T] to the set of parts of A and B respectively, such that $A(t_2) \subset A(t_1)$ (and $B(t_2) \subset B(t_1)$) if $t_i \le t_1 \le t_2 \le t_f$. In addition, we have A(t) = A and B(t) = B for $t \in [0, t_i]$, and $A(t) = B(t) = \phi$ for $t \in [t_f, T]$. In this way, the system (5), with $t \in [0, T]$ becomes a generalization of the whole fragmentation process modeled by (3)–(5).

2.1. On the per capita growth rate

The per capita growth rate $r: [0, \infty) \to (-\infty, \infty)$, as a function of the population density, assuming no migration rates, is the difference between per capita birth rate b and per capita death rate d, where $b, d: [0, \infty) \to [0, \infty)$ are assumed to be analytic on their whole domain. Developing $b[\cdot]$ and $d[\cdot]$ in Maclaurin series, we obtain

$$b[D] = b_0 + b_1 D + \sum_{k \ge 2} \frac{b_k}{k!} D^k \quad \text{and} \quad d[D] = d_0 + d_1 D + \sum_{k \ge 2} \frac{d_k}{k!} D^k,$$
(6)

where b_i and d_i , $i \in \{0, 1\}$, are positive numbers and $b_0 > d_0$. We assume also that $b[\cdot]$ is strictly decreasing and $d[\cdot]$ is strictly increasing, so that

there is a *density carrying capacity* D_{Ω}^* such that $b[D_{\Omega}^*] = d[D_{\Omega}^*]$.

2.2. Population densities in the transitional phase

To express $D_{A\cup B(t)}$ and $D_{A(t)\cup B}$ of (5) in other more interpretable terms, note that

$$D_{A\cup B(t)} = \frac{x_{A\cup B(t)}}{m(A\cup B(t))} = \frac{x_A(t) + x_{B(t)}(t)}{m(A) + m(B(t))}.$$

Introducing the hypothesis that the population in the region B(t) is a fraction of the abundance in *B* equal to the ratio of the sizes of the territories, we obtain

$$D_{A\cup B(t)} = \frac{x_A(t) + \eta(t)x_B(t)}{m(A) + \eta(t)m(B)},$$
(7)

with $\eta(t) = m(B(t))/m(B)$.

Similarly, the density $D_{A(t)\cup B}$ is given by

$$D_{A(t)\cup B} = \frac{x_A(t)\xi(t) + x_B(t)}{m(A)\xi(t) + m(B)},$$
(8)

where $\xi(t) = m(A(t))/m(A)$.

2.3. The unified equation

Replacing the population densities (7) and (8) in (5), we obtain explicitly the non-autonomous system of differential equations

$$\begin{cases} x'_{A} = x_{A} r \left[\frac{x_{A} + \eta(t) x_{B}}{m(A) + \eta(t)m(B)} \right], \\ x'_{B} = x_{B} r \left[\frac{x_{A}\xi(t) + x_{B}}{m(A)\xi(t) + m(B)} \right], \end{cases} t \in [0, T], \end{cases}$$
(9)

where η , ξ : $[0, T] \rightarrow [0, 1]$ are decreasing functions, such that $\eta(t) = \xi(t) = 1$ for any $t \in [0, t_i]$ and $\eta(t) = \xi(t) = 0$ for any $t \in [t_f, T]$).

The functions $\eta(\cdot)$ and $\xi(\cdot)$ can be interpreted as a measure of the degree of *connectivity* between the regions *A* and *B* at time *t*. A value of one for $\eta(\cdot)$ and $\xi(\cdot)$ means full connectivity between these subregions, and a value of zero means complete isolation between them due to the fragmentation. Hereafter, for simplicity, we assume that $\eta(\cdot)$ and $\xi(\cdot)$ are equal and differentiable.

3. Main results

Theorem 1. Let $(x_A(\cdot), x_B(\cdot))$ be a solution of (5) such that $x_A(t_i)/m(A) = x_B(t_i)/m(B)$. Then $x_A(t)/m(A) = x_B(t)/m(B)$ for each $t \in (t_i, t_f)$. In addition, $x_A(t) + x_B(t)$ satisfies (3).

$$P(x_A, x_B)(t) = (x_A(t) - x_B(t)) \left(\frac{x_A(t)}{m(A)} - \frac{x_B(t)}{m(B)} \right)$$

If $P(x_A, x_B)(t_i) > 0$ (resp. <), then $\chi(t) > x_A(t) + x_B(t)$ (resp. <) for each $t \in (t_i, t_i + \varepsilon)$, some $\varepsilon > 0$.

Proof. The proof is given in Appendix B.

Biological interpretation 2: Theorem 2 states that the fragmentation process could generate a decrease in population abundance, at least at the beginning of the process, particularly when

 $\min\{1, m_A/m_B\} < x_A(t_i)/x_B(t_i) < \max\{1, m_A/m_B\}.$

In addition, Theorem 2 shows the counterintuitive fact that there exist conditions under which the fragmentation process enhances the total population abundance for some time interval.

4. Highlighting consequences of fragmentation through numerical simulations

In order to simulate numerically the trajectories of population abundance determined by (9), we will consider a specific case for the per capita growth rate $r[\cdot]$, which is the well known Verhulst-Pearl logistic form. When the terms of higher order $k \ge 2$ are null in (6), then $b[D] = b_0 + b_1 \cdot D$ and $d[D] = d_0 + d_1 \cdot D$. Thus the per capita rate of growth, r[D] = b[D] - d[D], is determined by the expression $r[D] = r_0 - r_1 \cdot D$, where $r_0 = b_0 - d_0$ and $r_1 = d_1 - b_1$, with $d_1 > b_1$, because $r'[D] = b_1 - d_1 < 0$.

Due to the existence of the density carrying capacity D_{Ω}^{*} , it is natural to think of a population level K_{Ω} that determines this density. So, $K_{\Omega} = m(\Omega)(r_0/r_1)$ such that $r[K_{\Omega}/m(\Omega)] = 0$ is the carrying capacity of Ω . Then, Eq. (9) becomes

$$\begin{cases} x'_A = r_0 x_A \left\{ 1 - \frac{x_A + \eta(t) x_B}{K_A + \eta(t) K_B} \right\}, \\ x'_B = r_0 x_B \left\{ 1 - \frac{\xi(t) x_A + x_B}{\xi(t) K_A + K_B} \right\}, \end{cases} t \in [0, T],$$

$$(10)$$

where $K_C = m(C)(r_0/r_1)$, $C \in \{A, B\}$, are the carrying capacities of the subregions once the habitat fragmentation is completed.

In order to describe the global dynamics defined by the non-autonomous system (10), note that we have only the natural equilibria (0, 0) and (K_A , K_B), which are also equilibria of (3) and (4). In asymptotic terms, we have Eq. (4), where the origin is a repellor and (K_A , K_B) is globally asymptotically stable.

To visualize the dynamics on the interval (t_i, t_f) , we divide the set of states into six zones according to Table (11) and Fig. 2, where L(-) (respectively L(+)) means to be below (respectively above) the line L: $x_A + x_B = K_A + K_B$.

Z(1)	Z(2)	Z(3) $L(-)$	Z(4) L(+)	Z(5) L(+)	Z(6) $L(-)$
$x_A \le K_A$	$x_A \ge K_A$	$x_A \le K_A$	$x_B \le K_B$	$x_A < K_A$	$x_A > K_A$
$x_B \le K_B$	$x_B \ge K_B$	$x_B > K_B$	$x_A > K_A$	$x_B > K_B$	$x_B < K_B$

Proof. The proof is given in Appendix A.

Biological interpretation 1: The equality condition in Theorem 1 indicates that when the regions *A* and *B* have the same population densities at $t = t_i$, these densities persist over time during the fragmentation. In this case, the fragmentation process exerts no effect on the total population abundance.

Theorem 2. Let $(x_A(\cdot), x_B(\cdot))$ be a solution of (5) such that $x_A(t_i)/m(A) \neq x_B(t_i)/m(B)$, $\chi(\cdot)$ a solution of (3) on (t_i, t_f) such that $\chi(t_i) = x_A(t_i) + x_B(t_i)$ and

Then, given a point (x_A, x_B) in some Z(i), $i = 1, \dots, 6$, at some time $t \in (t_i, t_f)$, we present in Table (12) an overview of the signs of $x'_A(t)$ and $x'_B(t)$ at the same instant.

Z(i)	(1)	(2)	(3)	(4)	(5)	(6)
x'_A	+	-	+ & +	+ & -	- & +	+ & -
x'_B	+	-	+ & -	- & -	- & -	+ & +

In (12), a double sign (separated by &) in an entry means that the first sign corresponds to a first subinterval, and the next sign in the



Fig. 2. Left: Some trajectories defined by (10) with different initial states in six zones according to the signs of $x_A - K_A$, $x_B - K_B$ and $(x_A + x_B) - (K_A + K_B)$. Right: Case without fragmentation with the same initial conditions.

complementary interval, see Fig. 2.

Note that reordering the terms of (10), the signs of x'_A and x'_B are given respectively by the signs of $F = (K_A - x_A) + \eta(K_B - x_B)$ and $G = \eta(K_A - x_A) + (K_B - x_B)$.

In *Z*(1) we have $K_A - x_A > 0$ and $K_B - x_B > 0$, which are positive numbers. In *Z*(2) the argument is similar and x'_A and x'_B are negative.

In *Z*(3), we have $x_A < K_A$, $x_B > K_B$ and $(K_A + K_B) - (x_A + x_B) > 0$. Since *F* is equal to $[(K_A + K_B) - (x_A + x_B)] + (x_B - K_B)(1 - \eta)$, we obtain that x'_A is positive. In order to determine the sign of x'_B , note that $\lambda = (x_B - K_B)/(K_A - x_A)$ is a positive number less than one. So, there exists $t_1 \in [0, 1[$ such that if $t < t_1$ (respectively $t > t_1$), then $\eta > \lambda$ (respectively $\eta < \lambda$). Since $G = (\eta - \lambda)(K_A - x_A)$, we have $x'_B > 0$ (respectively <) if $t < t_1$ (respectively >).

In Z(4), we have that F is equal to $-\eta [(x_A + x_B) - (K_A + K_B)] - (1 - \eta)(x_A - K_A)(1 - \eta)$, a negative number, and so $x'_A < 0$. On the other hand, $\lambda = (K_B - x_B)/(x_A - K_A) < 1$ and $G = (\lambda - \eta)(x_A - K_A)$. Note that $t < t_1$ (respectively >) implies $\eta > \lambda$ (respectively <), *i.e.*, $x'_B < 0$ (respectively >).

Let us define $q = (K_A - x_A)/(x_B - K_B)$. In Z(5), we have $F = (K_B - x_B)$ and G equals $-[(x_A + x_B) - (K_A + K_B)] - (1 - \eta)[K_A - x_A]$. Then $x'_B < 0$ and $x'_A < 0$ or $x'_A > 0$ depending on whether $q < \eta$ or $q > \eta$, that is, $t < t_2$ or $t > t_2$, where $\eta(t_2) = q$.

Finally, in *Z*(6), since *F* and *G* are, respectively, $(K_B - x_B)(\eta - q)$ and $(K_B - x_B)(1 - \eta q)$, it follows that $x'_B > 0$ and $x'_A > 0$ (respectively <) if $t < t_2$ (respectively >).

Let us consider an interval of fragmentation $[t_i, t_f] = [20, 70]$ as a subset of a horizon time [0, T] = [0, 100]. We take the parameters that follow:



-0	0	-1	1	(1)	(2)	
2/10	1/10	1/100	4/100	180	30	

Note that with these parameters, $r_0 = 1/10$, $r_1 = 3/100 K_A = 600$ and $K_B = 100$.

Assuming a linear connectivity function η $(t) = \xi(t) = (t_f - t)/(t_f - t_i), t \in [t_i, t_f]$, and initial conditions $x_A(0) = 100$ and $x_B(0) = 50$, Fig. 3 compares the total abundances of the cases with and without fragmentation. Note that, $x_A(20) = 312$ and $x_B(20) = 156$ then $1/6 = m(B)/m(A) < x_B(20)/x_A(20) < 1$, which is consistent with Theorem 2 part (b).

More details on the behavior of an alternative model of $r[\cdot]$ are given in Appendix C.

From Theorem 2 it follows that the largest effects exerted by the fragmentation process on population abundances are exhibited well before the system reach the steady state. In this section, we analyze by numerical means how habitat fragmentation affects the long-term behavior of a population that is periodically perturbed in its death rate at migration instance. For this goal, we will use a modified version of system (10):

$$\begin{cases} x'_{A}(t) = r_{0}x_{A}(t)\left(1 - \frac{x_{A}(t) + \eta(t)x_{B}(t)}{K_{A} + \eta(t)K_{B}}\right) \\ x'_{B}(t) = r_{0}x_{B}(t)\left(1 - \frac{x_{A}(t)\eta(t) + x_{B}(t)}{K_{A}\eta(t) + K_{B}}\right) \end{cases}, \quad t \neq \tau_{k} \in [t_{i}, t_{f}] \subseteq [T_{0}, T_{1}] \\ x_{A}(t^{+}) = (1 - p)x_{A}(t) + qx_{B}(t) - \mu x_{A}(t) \\ x_{B}(t^{+}) = (1 - q)x_{B}(t) + px_{A}(t) - \mu x_{B}(t) \end{cases}, \quad t = \tau_{k} \in [t_{i}, t_{f}] \subseteq [T_{0}, T_{1}]$$

$$(13)$$



Fig. 3. The possibility that the total abundance $x_A(\cdot) + x_B(\cdot)$ in the fragmentation model (green line) is greater than the abundance without fragmentation (red dashed line), at least during the interval of fragmentation [20, 70]. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



Fig. 4. Long-term decrease in population abundance driven by the habitat fragmentation process, in a population subjected to periodical perturbation on its death rate. The *x*-axis shows the time interval between successive perturbation events, $\Delta \tau$, and the *y*-axis shows the intensity of the perturbation, μ . Negative/positive values (see color scale) indicate decreases/ increases in population abundances integrated over the last fifty time steps. Parameter values as follows. (a) p = q = 0.1, $K_A = 600$, $K_B = 100$; (b) p = q = 0.1, $K_A = 200$, $K_B = 500$; (c) p = q = 0.2, $K_A = 600$, $K_B = 100$; (d) p = q = 0.2, $K_A = 200$, $K_B = 500$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

This is an impulsive system (Córdova-Lepe, 2007; Del Valle et al., 2012) that exhibits logistic population growth, with the same intrinsic growth rate r_0 in the two patches. At certain time instants τ_k equally spaced during the transition phase of the fragmentation process, fractions p and q of subpopulations in A and B migrate to the other patch, and some fraction μ in each subpopulation dies as a consequence of the perturbation. With $\mu = p = q = 0$, system (13) reduces to system (10).

Using the time horizon $t \in [T_0, T_1]$, a linear connectivity function $\eta(t) = \frac{t_f - t}{t_f - t_i}$ with time values, $T_0 = 0$, $t_i = 0$, $T_1 = t_f = 200$, where $r_0 = 1/10$, $r_1 = 3/10$, and initial condition $x_A(T_0) = 100$, $x_B(T_0) = 50$, we performed computer simulations of system (13) to show some model behaviors (Fig. 4). Fig. 4 shows how the negative effect of fragmentation on population abundance increases with perturbation intensity (μ). Besides this, the time interval between successive perturbation events $(\Delta \tau)$ also exerts a marked influence on the magnitude of the fragmentation impact on population abundance. The range of $\Delta \tau$ for which fragmentation exerts its stronger negative effect increases with μ , from near zero for the lowest μ values to intermediate values of about 20–40 time units for highest μ values. These effects exerted by μ and $\Delta \tau$ were stronger with higher values of migration rates p and q (Fig. 4c and d) and with higher differences between carrying capacities K_A and K_B (Fig. 4a and c). Note also that for low μ and high $\Delta \tau$ values, we found that habitat fragmentation increased population abundance summed over the two patches, even so this effect was slight in magnitude (Fig. 4a–d).

5. Discussion

The analytical results of our study reveal that, in general, habitat fragmentation acting only through suppressing connectivity among regions affects the abundances of involved populations during some time interval. A restricted case does not follow this rule: when initial population density is homogeneous across habitat regions that will get isolated. Whenever population density is different between regions A and B at the beginning of the fragmentation process, population abundances will be either enhanced or depleted by fragmentation, before the population reaches its steady state.

Based on our analysis we conjectured that, given that the effects of habitat fragmentation are mostly exhibited in a transient phase of population dynamics, they should be especially important in populations whose asymptotic dynamics is delayed by perturbations exerted during the fragmentation process. Therefore, we performed numerical simulations on a version of our mathematical model aimed at highlighting the effects of habitat fragmentation in perturbed populations, in a sample of the parameter space. Our numerical results confirmed our expectations, showing that habitat fragmentation via connectivity loss could exert both negative and positive effects on total population density, although the positive effects are expected to be of low intensity. In perturbed populations, strong adverse effects of habitat fragmentation are evident. The magnitude of these effects was markedly dependent on perturbation intensity and frequency, but also on migration rates and heterogeneity in the carrying capacities of the patches. In general terms, our analytical and numerical results suggest that habitat fragmentation in their more restricted sense (connectivity loss), independent on habitat loss, edge effects and other related processes, exert important -and most likely adverse- effects on population abundances.

The process of habitat fragmentation involves a set of phenomena besides the isolation of habitat regions per se. Among the most important ones, habitat loss and edge effects are known to exert severe effects on biodiversity (Fahrig, 2003; Haddad et al., 2015). Nevertheless, the empirical studies show conflicting results respect to the main effect of habitat fragmentation and connectivity loss as a driver of biodiversity changes (Debinski and Holt, 2000; Ibá nez et al., 2014). In particular, it has been found that connectivity loss, once isolated from habitat loss and degradation, can exert either negative, null or indeed positive effects on populations (Caley Julian et al., 2001; Fahrig, 2003), as our model predicts. However, for a large portion of the parameter space, habitat fragmentation via loss of connectivity exerts negative effects on population abundance. This was particularly evident when the simulated population was subjected to periodic perturbations, so extending its transient phase.

Recently. Haddad et al. (2015) reviewed the best available experimental results reporting various ecological effects of fragmentation, including population abundances of species. The experiments were conducted on evergreen broadleaf forests (The Biological Dynamics of Forest Fragments Project BDFFP, Brazil, initiated in the early 1980s and The Wog Wog Habitat Fragmentation Experiment WW, Australia, initiated in 1987), shrub (Kansas Fragmentation Experiment KFE, USA, initiated in 1984) and grassland (Savannah River Site experiment SRS. USA, initiated in 1993 and The Moss Fragmentation Experiments MFE. UK and Canada, initiated in 1995) ecosystems (see details in Haddad et al., 2015). All these studies reported results from long-term experiments (>20 years) which covered entire ecosystems. From a total of eight results on population abundances, six of them gave negative effects while other two gave positive effects. Decreases in abundances as a result of habitat fragmentation were observed in birds (BDFFP), spiders (KFE), insects (KFE), butterflies (SRS), plants (SRS) and microarthropods (MFE). On the other hand, increases in abundance driven by fragmentation were observed in plants (KFE) and beetles (WW). However, when the effect of connectivity loss was isolated, there was a clear trend toward negative effects, in line with our findings.

Our results suggest that habitat connectivity loss can be a cause of strong impact on population abundance in stochastic environments, where the occurrence of perturbations of diverse nature is the rule and not the exception.

Of course, for this effect to occur fragmentation should impede movements of individuals across non-connected patches. As claimed in

Appendix A. Proof of Theorem 1

Considering the integral representations for the system of equations (5), we have

$$|\alpha(t) - \beta(t)| \le |\alpha(t_i) - \beta(t_i)| + \int_{t_i}^{t_i} |\Delta(s)| \mathrm{d}s, \quad t \in [0, T],$$

where $\alpha(\cdot) = x_A(\cdot)/m_A$, $\beta(\cdot) = x_B(\cdot)/m_B$ and

 $\Delta(s) = \alpha \{ r [D_{A \cup B(s)}] \} - \beta \{ r [D_{A(s) \cup B}] \}.$

Using the Maclaurin series introduced in (6), it follows that

at

$$\Delta(s) = \sum_{k \ge 0} \frac{\eta_k}{k!} \{ \alpha(s) [D_{A \cup B(s)}]^k - \beta(s) [D_{A(s) \cup B}]^k \},\$$

with $n_k = b_k - d_k$, $k \ge 0$. Denoting by $\omega_k(\alpha, \beta)(s)$ the summands in parentheses in the above equality, it follows that

$$|\Delta(s)| \leq \sum_{k\geq 0} \frac{|\eta_k|}{k!} |\omega_k(\alpha, \beta)(s)|.$$

Assuming $\lambda = m(A)/m(B)$, the densities defined in (7) and (8) can be written as

$$D_{A\cup B(s)}(\eta) = \frac{\alpha + \eta \lambda^{-1} \beta}{1 + \eta \lambda^{-1}}$$
 and $D_{A(s)\cup B}(\eta) = \frac{\beta + \eta \lambda \alpha}{1 + \eta \lambda}$.

It is straightforward to prove that $D(\mu) = D_{A \cup B(s)}(\mu) = D_{A(s) \cup B}(\mu^{-1})$, for $\mu \in \{\eta, \eta^{-1}\}$. In addition, the function $D_{A \cup B(s)}(\eta)$ (respectively $D_{A(s) \cup B}(\eta)$) is increasing if only if $\alpha \leq \beta$ (respectively $\alpha \geq \beta$). Thus,

$$\begin{cases} \alpha < D(\eta) < D(\eta^{-1}) < \beta, & \text{if} \alpha \le \beta, \\ \beta < D(\eta^{-1}) < D(\eta) < \alpha, & \text{if} \beta \le \alpha. \end{cases}$$

Then the function $\omega_k(\alpha(\cdot), \beta(\cdot)) = 0$ if $\alpha(\cdot) = \beta(\cdot)$, and

$$\omega_k(\alpha,\beta)| = \begin{cases} \alpha \cdot \left[D\left(\frac{1}{\eta}\right) \right]^k - \beta \cdot [D(\eta)]^k, & \text{if } \alpha < \beta, \\ \beta \cdot [D(\eta)]^k - \alpha \cdot \left[D\left(\frac{1}{\eta}\right) \right]^k, & \text{if } \alpha > \beta. \end{cases}$$

The inequalities in (15) imply the bounds

Caley Julian et al. (2001), there could be species whose organisms are insensitive to fragmentation due to their high mobility. Therefore, the same physical force of habitat division could affect the connectivity of species among patches in diverse degrees. This study opens opportunities for extending our model to more realistic scenarios, such as multispecific assemblages with varying degrees of organism's mobility, simultaneous habitat divisions that occur at different rates, and including other environmental phenomena that often co-occur with habitat division, such as habitat loss, degradation, and biological invasions. Fragmentation of both terrestrial and aquatic ecosystems will continue to occur on earth, for which it is necessary to develop a deeper understanding of the nature, underlying mechanisms and ecological consequences of this process, in order to build a more solid, explanatory and predictive theory of habitat fragmentation, useful also for designing better management practices.

6. Code availability

For simulation analysis we used MATLAB version 2016a (The Mathworks Inc., Natick, Massachusetts). The complete code is available from the authors upon request.

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(14)

$$|\omega_k(\alpha, \beta)| \le \begin{cases} \alpha^{k+1} - \beta^{k+1}, & \text{if} \alpha < \beta, \\ \beta^{k+1} - \alpha^{k+1}, & \text{if} \alpha > \beta. \end{cases}$$

Hence

 $|\omega_k(\alpha,\beta)(s)| \leq |\alpha^{k+1}(s) - \beta^{k+1}(s)| \leq |\alpha(s) - \beta(s)| \sum_{i=0}^k \alpha^{k-i}(s)\beta^i(s).$

Let us define $M = \max\{D_A^* + D_B^*, D_A^*(t_i), D_B^*(t_i)\}$. Then $\alpha(t)$, $\beta(t) \le M$ for each $t \ge t_i$. Indeed, if there exists $t_1 > t_i$ with $\alpha(t_1) > M \ge \alpha(t_i)$, then there exists $t_2 \in (t_i, t_1]$ such that $\alpha(t_2) > M$ and $\alpha'(t_2) > 0$. However, $\alpha(t_2) > D_A^* + D_B^*$ implies $\alpha'(t_2) < 0$, a contradiction. Similarly, it is possible to prove that $\beta(t) \le M$.

Then $\alpha(\cdot)$ and $\beta(\cdot)$ are bounded functions. Therefore, from (16), we have $|\omega_k(\alpha, \beta)(s)| \le |\alpha(s) - \beta(s)|(1+k)M^k$, which implies

$$|\Delta(s)| \le |\alpha(s) - \beta(s)| \sum_{k \ge 0} \gamma_k, \quad s \in [t_i, T],$$
(17)

where $\gamma_k = |r_k(1 + k)M^k/k!$. Note that $\sum \gamma_k$ converges because the series $\sum r_k D^k$ does.

Therefore, there exists $\overline{M} > 0$ such that $|\Delta(s)| \le \overline{M}|\alpha(s) - \beta(s)|$, for each $s \ge t_i$. Using (14) and Gronwall's Inequality (Sotomayor, 1979), we obtain that $|\alpha(t) - \beta(t)| \le |\alpha(t_i) - \beta(t_i)|e^{\overline{M}(t-t_i)}$, for any $t \in [t_i, T]$. Since $\alpha(t_i) = \beta(t_i)$, we have $\alpha(\cdot) = \beta(\cdot)$. So the first part of (a) is proved.

Finally, since $\alpha(\cdot) = \beta(\cdot)$, we have that $D_{A\cup B(t)} = D_A$ and $D_{A(t)\cup B} = D_B$ for $t \in [0, T]$. Then $x'_C = x_C r[D_C]$, for any $C \in \{A, B\}$. Therefore, $x(\cdot) = x_A(\cdot) + x_B(\cdot)$ satisfies $x' = x r[D_\Omega] + x_A r[D_A] + x_B r[D_B] - (x_A + x_B) r[D_\Omega]$ and it is straightforward $(D_A = D_B = D_\Omega)$ to conclude (3).

Appendix B. Proof of Theorem 2

We will compare the first two derivatives of $\chi(\cdot)$ with those of the sum $x_A(\cdot) + x_B(\cdot)$. Note that at $0 \le t \le t_i$, we have

$$x'_{A} + x'_{B} = x_{A}r[D_{A\cup B(t)}] + x_{B}r[D_{A(t)\cup B}].$$

Since $\eta(\cdot) = 1$ on $[0, t_i]$, the right side of (18) is equal to $x_A r[D_{A\cup B}] + x_B r[D_{A\cup B}] = (x_A + x_B)r[D_\Omega]$. That is, $\chi' = x'_A + x'_B$ at $t \le t_i$. Moreover, for $t \in [t_i, t_i]$, we have

$$x_p'' = x_p' r [D_{p \cup q(t)}] + x_p r' [D_{p \cup q(t)}] D'_{p \cup q(t)}$$

where if p = A (respectively *B*), then q = B (respectively *A*).

Developing $D'_{p\cup q(t)}$ from (19) and evaluating at $t = t_i$ and using the fact that $\chi(\cdot)$ and $x_p(\cdot) + x_q(\cdot)$, and their first derivatives, have the same value, we obtain

 $D'_{\Omega} = \{(\chi' + \eta' x_q)m(\Omega) - \chi\eta' m(q)\}/m^2(\Omega),$

i.e., the expression (19) can be represented by

 $x_p'' = x_p' r [D_\Omega] + x_p r' [D_\Omega] \{ (\chi' + \eta' x_q) m(\Omega) - \chi \eta' m(q) \} / m^2(\Omega).$

Then

 $x_p'' + x_q'' = \chi' r[D_\Omega] + \frac{r'[D_\Omega]}{m^2(\Omega)} \{ \chi' \chi m(\Omega) + 2x_p x_q \eta' m(\Omega) - (x_p m(q) + x_q m(p)) \eta' \chi \}.$

Therefore,

$$\chi'' - (x_p'' + x_q'') = -\frac{r'[D_{\Omega}]}{m^2(\Omega)} \eta' \{ 2x_p x_q m(\Omega) - \chi(x_p m_q + x_q m_p) \}.$$

That is,

$$\chi'' - (x_A'' + x_B'') = \frac{r'[D_\Omega]}{m^2(\Omega)} m_A m_B \eta'(x_A - x_B) \left(\frac{x_A}{m_A} - \frac{x_B}{m_B}\right).$$

So that $x_A(\cdot) + x_B(\cdot) > \chi(\cdot)$ in a neigbourhood to the right of $t = t_i$ if $(x_A - x_B)(x_A/m_A - x_B/m_B) < 0$, which is a condition equivalent to those given in Theorem 2.

Appendix C. Rational Smith's Daphnia magna per capita rate

In Smith (1963), Smith, in order to describe the growth of D. magna, introduces the following per capita rate:

$$r[D] = r_0 \frac{D_{\Omega}^* - D}{D_{\Omega}^* + c \cdot D}, \quad D > 0,$$

where r_0 and c are some positive constants. Note that, the above function is analytic on $[0, \infty +)$ and its series development is given by $r[D] = r_0 \varphi(D/D_{\Omega}^*)$, where $\varphi(\omega) = 1 - \omega(1 + c)(1 - \omega c + (\omega c)^2 - (\omega c)^3 + \cdots)$, when $\omega < c^{-1}$.

With this per capita rate, the system (9) can be expressed as

$$\begin{cases} x'_A = r_0 x_A \left\{ \frac{(K_A + \eta K_B) - (x_A + \eta x_B)}{(K_A + \eta K_B) + c (x_A + \eta x_B)} \right\} \\ x'_B = r_0 x_B \left\{ \frac{(K_A \xi + K_B) - (x_A \xi + x_B)}{(K_A \xi + K_B) + c (x_A \xi + x_B)} \right\} \\ \end{cases} \quad t \in [0, T],$$

(20)

(18)

(19)

(16)



Fig. 5. Case where the total population at the beginning of the fragmentation process exceeds for some time the abundance that would have obtained without fragmentation.

where $K_C = m(C)D_{\Omega}^*$, with $C \in \{A, B\}$, are the subregional carrying capacities when the habitat fragmentation is completed. Let us consider an interval of fragmentation $[t_i, t_f] = [0, 50]$, as a subset of [0, T] = [0, 100], and the parameters that follow:

b_0	d_0	D^*_Ω	m(A)	m(B)
2/10	1/10	10/3	180	30

Note that with these parameters, $r_0 = 1/10$, $K_A = 600$, $K_B = 100$ and c = 0.5.

Fig. 5 illustrates the case of a linear connectivity function $\eta(t) = \xi(t) = (t_f - t)/(t_f - t_i)$, $t \in [t_i, t_f]$, and initial conditions $x_A(0) = 100$ and $x_B(0) = 50$. Note that, $x_B(0)/x_A(0) = 1/2$ and $m_B/m_A = 1/6$, then we are in case (a) of Theorem 2.

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