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

Fernando Córdova-Lepe[a], Rodrigo Del Valle[a,*], Rodrigo Ramos-Jiliberto[b,c]

[a] Departamento de Matemática, Física y Estadística, Universidad Católica del Maule, Av. San Miguel 3605, Talca, Chile
[b] GEMA Center for Genomics, Ecology & Environment, Universidad Mayor, Camino La Pirámide 5750, Huechuraba, Santiago, Chile
[c] Programas de Postgrado, Facultad de Ciencias, Pontificia Universidad Católica de Valparaíso, Av. Brasil 2950, Valparaíso, Chile

A B S T R A C T

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
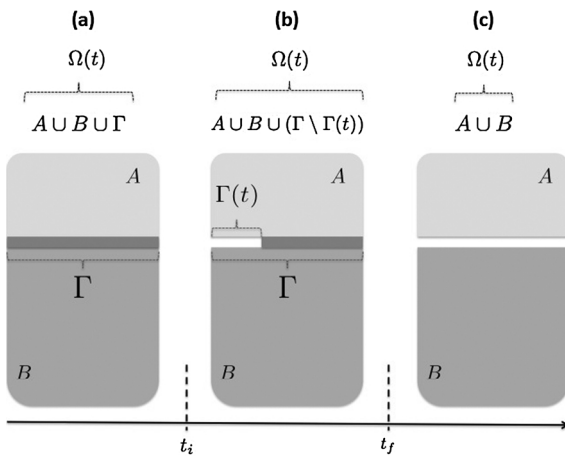

Fig. 1. Three snapshots of the fragmentation process through time, occurring on the habitat Ω: (a) state of the habitat before the beginning of the fragmentation process, $\Omega(t)$ composed of subregions A, B and a shared border Γ; (b) state of Ω in a time just after the initiation of the fragmentation 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 $t \geq 0$ 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 $B(t) = \Omega(t)\backslash A(t)$ 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

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

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 $\alpha: (t_i, t_f) \to \Omega$ such that $\alpha(t_i^+)$ and $\alpha(t_f^-)$ exist in $\mathbb{R}^2\backslash\Omega$.

Writing $\Gamma(t) = \{\alpha(s): s \in (t_i, t)\}$ with $t \in (t_i, t_f)$, we have that, at any moment t of the process, the habitat is represented by the set $\Omega(t) = \Omega\backslash\Gamma(t)$. 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 ($0 \leq t \leq t_i$): 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

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

which is another form of Eq. (1).

Fragmented habitat ($t_f \leq t \leq T$): 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,

$$\begin{cases} x'_A = x_A\, r\,[D_A], \\ x'_B = x_B\, r\,[D_B], \end{cases} \quad t \in [t_f, T]. \tag{4}$$

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:

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

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 B at 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 $t_i \leq t_1 \leq t_2 \leq t_f$. 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

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

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