



# Modelling plant population size and extinction thresholds from habitat loss and habitat fragmentation: Effects of neighbouring competition and dispersal strategy



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## ABSTRACT

Habitat destruction is a key determinant of species extinction. Its principle components, habitat fragmentation and habitat loss, affect species persistence in landscapes, but few models have investigated how dispersal type and intraspecific competition (crowding effect) modulate this. If dispersal type or crowding changes extinction thresholds, then fragmentation and habitat loss might act differently on different species. Here we generate fragmented landscapes by varying the orthogonal neighbouring correlation between suitable and unsuitable habitat. We show that local dispersers undergo a strong negative impact of habitat fragmentation (lower occupancy of suitable sites), but only under severe habitat loss. In contrast, global dispersal eliminated fragmentation effects through random establishment. Both fragmentation and crowding effects enhanced the extinction risk of species that spread their seeds at close range, while long-range dispersers were not influenced. However, fragmentation improved the persistence of global dispersers that are highly sensitive to crowding, probably through reduced intraspecific competition. With respect to species conservation, our results suggest that random habitat destruction is a more serious threat to species persistence than clustered habitat destruction. Moreover, as species responses to habitat fragmentation depend on dispersal type and sensitivity to crowding, fragmented landscapes with different properties may accommodate different species.

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## 1. Introduction

Habitat destruction is considered one of the most influential factors contributing to species extinction (Ehrlich, 1995; Thomas and Morris, 1995; Fahrig, 2001). Understanding its effects has consequently become a central issue in ecology and conservation (Tilman and Kareiva, 1997; Dieckmann et al., 2000). In the view of Fahrig (2002, 2003), habitat destruction includes two main components: habitat loss and habitat fragmentation. The former is the reduction in the amount of available habitat, while the latter refers to the breaking apart and thus the change in the spatial arrangement of

the remaining habitat. To date, many theoretical mechanisms have been proposed whereby habitat destruction can cause the decline of population persistence, and significant advances – mostly through modelling – have been made in our understanding of how species respond to it (Dytham, 1995; Bascompte and Solé, 1996; Boswell et al., 1998; Hill and Caswell, 1999; With and King, 1999; Travis and Dytham, 2004; McInerney et al., 2007; Solé and Bascompte, 2007). In most of these models, the effects of habitat loss far outweigh those of habitat fragmentation (Fahrig, 1997, 2002; Flather and Bevers, 2002). However, Hiebeler (2000, 2004) and Ovaskainen et al. (2002) simulated major effects of fragmentation on species persistence in spatially correlated landscapes where species occur in aggregated patterns. The importance of habitat configurational complexity for species persistence therefore remains ambiguous (Ewers and Didham, 2006).

The substantial body of empirical work concerning the influence of habitat fragmentation on species persistence, on the other hand, has demonstrated positive as well as negative effects (Fahrig,

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2002, 2003; Ewers and Didham, 2006). This further indicates that there are still many facets to the study of fragmentation that remain untested in modelling work (Ewers and Didham, 2006). Given that most of the models referred to above predict consistently negative effects when habitats are broken up, they may have ignored certain species traits or processes that induce positive responses (Fahrig, 2002). Species dispersal strategy or intraspecific competition would be candidates for these missing elements in current models (McInerny et al., 2007; North and Ovaskainen, 2007; Liao et al., 2013a). For example, species characterized by distance-limited dispersal may be negatively influenced by habitat fragmentation (Hiebeler, 2000; Snyder and Chesson, 2003; McInerny et al., 2007; Bonte et al., 2010; Débarre and Lenormand, 2011), while species exhibiting long-range dispersal would be able to persist more easily (With and King, 1999; Fahrig, 2001; Ewers and Didham, 2006; McInerny et al., 2007; Liao et al., 2013a). Consequently, dispersal modes should be taken into account when predicting species responses to habitat fragmentation. By analyzing the evolution of dispersal traits in density-dependent populations, Bonte et al. (2010) showed that the proportion of individuals performing global dispersal actually increases in more fragmented landscapes. The reason why intraspecific competition could be important for fragmentation effects can be understood from the idea that conspecific individuals that compete heavily with each other would benefit from the breaking down of monospecific clumps, which fragmentation promotes (North and Ovaskainen, 2007). A study that investigated the combined effects of dispersal type and intraspecific competition (i.e., crowding effect) on species persistence was conducted by North and Ovaskainen (2007), who observed positive effects of landscape heterogeneity by varying patch size and quality. However, few theoretical studies have systematically explored whether the interaction between neighbouring competition and dispersal traits influences species extinction thresholds in fragmented landscapes.

The current study extends the spatially explicit modelling methods of Hiebeler (2000) by simultaneously introducing the crowding effect and seed dispersal traits of plant species (i.e., local vs. global dispersal). Using the landscape generation algorithm of Hiebeler (2000, 2007), we first construct fragmented landscapes applying the principle of nearest neighbourhood correlations. Next, we model species persistence in response to landscape fragmentation by simulating each individual's birth and death (intrinsic mortality). Births are generated by local and/or global seed dispersal, with local dispersal limited to nearest neighbours and global dispersal being random across the entire landscape. The model assumes that seed production is negatively influenced by the crowding effect because of resource competition (Harada and Iwasa, 1994, 1996). With the model, we explore how dispersal type (local or global) and crowding effect modulate the impact of habitat fragmentation and habitat loss on population persistence and extinction threshold.

## 2. Methods

### 2.1. Landscape generation

We simulate landscapes with a two-dimensional square lattice of  $L \times L = 100 \times 100$  cells ( $L$  is the length of the lattice), which acts like a torus to avoid the edge effect. Each cell – further referred to as “site” – has a unit area of  $1 \times 1$ , and can be either vacant or occupied by an individual. To introduce fragmentation, we define two types of habitat  $E_1$  and  $E_2$ , where only  $E_1$  sites can be occupied by individuals (density  $\rho_{E_1}$ , with  $0 \leq \rho_{E_1} \leq 1$ ) while  $E_2$  sites are unsuitable for plant growth (habitat loss, density  $\rho_{E_2}$ , with  $0 \leq \rho_{E_2} \leq 1$ ); note that  $\rho_{E_1} + \rho_{E_2} = 1$ . The degree of fragmentation of a given habitat (either  $E_1$  or  $E_2$ ) is negatively related to

its clumping degree. Clumping degree is expressed by the local density  $q_{iji} = \rho_{ij}/\rho_i$  with  $i \in \{E_1, E_2\}$ , where  $q_{iji}$  ( $0 \leq q_{iji} \leq 1$ ) is the conditional probability of the nearest neighbour of an  $i$ -site being also an  $i$ -site (Matsuda et al., 1992),  $\rho_{ij}$  ( $0 \leq \rho_{ij} \leq 1$ ) denotes the density of  $i$ - $i$  pairs, and  $\rho_i$  represents the density of  $i$  sites. Degree of fragmentation itself is defined as  $1 - q_{iji}$ . For simplicity, we use von Neumann neighbourhood with  $z = 4$  neighbours per site. According to the landscape generation algorithm of Hiebeler (2000, 2007),

$$q_{iji} \geq 2 - \frac{1}{\rho_i}, \quad (i = E_1 \text{ or } E_2). \quad (1)$$

This means that the valid range of the clumping degree of a given habitat type depends on its global density.

Using Hiebeler's algorithm (2000, 2007), we produce three levels of habitat fragmentation ( $1 - q_{E_1/E_1}$ ), while keeping habitat availability  $\rho_{E_1}$  constant (Fig. 1). In the special case where  $q_{E_1/E_1} = \rho_{E_1}$  (Fig. 1b), the pattern of the two habitats ( $E_1$  and  $E_2$ ) is random (Hiebeler, 2000). If  $q_{E_1/E_1} < \rho_{E_1}$ , the suitable  $E_1$  sites have less orthogonal neighbours with themselves, yielding an overdispersed pattern with many small isolated  $E_1$ -patches (high fragmentation in Fig. 1a). If  $q_{E_1/E_1} > \rho_{E_1}$ , the  $E_1$ -sites tend to occur together, shaping an aggregated distribution (low fragmentation in Fig. 1c).

### 2.2. Lattice-structured population model

In this section we apply a discrete-time model to simulate plant species persistence in the fragmented landscapes defined above. As individuals denoted as  $I$  are introduced, each site can be in one of three states:  $E_1$ ,  $E_2$  or  $I$ . In each time step, every occupied site produces up to  $s$  seeds, where  $s$  is the intrinsic seed production rate. The actual number of seeds produced is a decreasing function of the local density of individuals. Assume seeds are distributed at random within a dispersal range, as discussed below. For simplicity, two extreme types of dispersal – global and local – are included in the model. A mortality rate of  $d$  per time step is used, meaning that an occupied site will remain occupied in the following time step with probability  $1 - d$ .

Under global dispersal, seeds are randomly distributed across the landscape. The average number of seeds received by each site equals

$$\lambda = s \cdot \rho_I \cdot (1 - \alpha \cdot q_{I/I}), \quad (2)$$

where  $s$  is the intrinsic seed production rate per individual of population  $I$ , and  $\rho_I$  is the population density. The term  $\alpha \cdot q_{I/I}$  represents the mean crowding effect on seed production, i.e., the negative influence of neighbours due to resource competition (Harada and Iwasa, 1994, 1996). The crowding effect is consequently determined by the average clumping degree ( $q_{I/I}$ ) and the species sensitivity to crowding ( $\alpha$ , with  $0 \leq \alpha \leq 1$ ). Given the random distribution of the seed rain under global dispersal, the number of seeds landing on each site follows a Poisson distribution with mean  $\lambda$ . We assume that all individuals are genetically identical with respect to germination and seedling survival, and that seed production refers to viable seeds that germinate and make it to the adult stage (Harada and Iwasa, 1994; Liao et al., 2013b). Consequently, the probability of an empty  $E_1$ -site being occupied equals

$$P_1 = 1 - \exp(-\lambda), \quad (3)$$

where  $\exp(-\lambda)$  is the probability of an empty site receiving no seeds.

A different equation is needed when a population regenerates through local dispersal to the nearest neighbouring sites ( $z = 4$ ). In

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