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# Species persistence in landscapes with spatial variation in habitat quality: A pair approximation model



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## HIGHLIGHTS

- We model species persistence in landscapes with spatial variation in habitat quality.
- Habitat heterogeneity enhances species persistence relative to habitat homogeneity.
- Habitat configurational fragmentation improves persistence of global dispersers.
- Fragmentation and density dependence promote extinction risk of local dispersers.
- Species with density dependence exhibit diverse responses to habitat fragmentation.

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## ABSTRACT

Habitat degradation has become a major threat to species persistence. Although several models have explicitly integrated habitat quality into metapopulation dynamics, we still lack knowledge of the spatial variability of species persistence which may result from the clustering of habitat patches of differing quality. Here we construct both pair approximation (PA) and cellular automaton (CA) models for species persistence in homogeneous versus heterogeneous landscapes. Heterogeneous landscapes are generated by varying the orthogonal-neighbour correlation between two different-quality habitats. In our simulations, the PA model exhibits similar population dynamics to the CA model, though it overestimates species persistence due to the doublet approximation neglecting correlation beyond nearest neighbours. Generally, landscape heterogeneity enhances species persistence relative to landscape homogeneity, especially with enlarging habitat-quality difference. This indicates that models based on homogeneous landscapes may overestimate species extinction rate. In heterogeneous landscapes, habitat clumping does not influence global dispersers because of random establishment, although it does promote the persistence of local dispersers, especially under severe habitat degradation. However, habitat configurational fragmentation improves the persistence of global dispersers that are highly sensitive to local crowding, probably by reducing density dependence, but this positive fragmentation effect on local dispersers is overshadowed by the stronger negative border effect on impeding local extension. Furthermore, increasing density dependence promotes the extinction risk of local dispersers, while global dispersers are not influenced. For conservation and habitat management, our results suggest that minimising random anthropogenic disturbance should take priority over increasing the connectivity of good-quality habitat, as random habitat degradation poses a more serious threat to species persistence than clustered habitat degradation. Owing to species' diverse responses to habitat configurational fragmentation, landscapes with different properties may accommodate different species.

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## 1. Introduction

Many populations now face the threat of habitat degradation (Sala et al., 2000; Griffen and Drake, 2008). The process of degradation may result from either reduction in habitat size

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through habitat loss or fragmentation, or decline in habitat quality through loss of resources or anthropogenic disturbance (Griffen and Drake, 2008). An increasing number of both theoretical and empirical studies have already focused on the relative importance of habitat loss versus habitat fragmentation on species persistence, and significant progress has been made (see the reviews by Harrison and Bruna, 1999; Fahrig, 2002, 2003; Crooks and Sanjayan, 2006; Ewers and Didham, 2006; Fischer and Lindenmayer, 2007; Lindenmayer and Fischer, 2007). In most of these studies, the distance-limited dispersers can tolerate more habitat loss if the remaining habitat is highly connected, while the longer-range dispersers suffer less from the effects of habitat fragmentation (Dytham, 1995; Pearson et al., 1996; With and King, 1999a, b; Hill and Caswell, 1999; Fahrig, 2001, 2002; Flather and Bevers, 2002; Ovaskainen and Hanski, 2003; McInerney et al., 2007). However, habitat loss and fragmentation are extreme cases of habitat degradation, and real landscapes rarely consist of neatly divided patches of ‘habitat’ and ‘non-habitat’ (Drielsma and Ferrier, 2009). Usually, habitat degradation coincides with reduction in habitat quality so that most landscapes exhibit at least some level of habitat variegation (i.e., varying suitability for species) (McIntyre and Barrett, 1992; Fischer and Lindenmayer, 2006; Drielsma et al., 2007; Lindenmayer and Fischer, 2007).

Indeed, increasing empirical evidence confirms that habitat quality plays a significant role in regulating population dynamics in heterogeneous landscapes (Thomas et al., 2001; Adriaens et al., 2009; Drielsma and Ferrier, 2009; Hodgson et al., 2009; Mortelliti et al., 2010). For instance, habitat quality might dominate the long-term metapopulation dynamics, and could predict species colonisation and extinction dynamics better than patch size and isolation alone (Root, 1998; Thomas et al., 2001; Fleishman et al., 2002; Franken and Hik, 2004). Intuitively, decreasing habitat quality can be expected to result in a lower fitness for a species, reducing population occupancy through increased mortality and/or lower fecundity (Felton et al., 2003; Hazell et al., 2004; Mortelliti et al., 2010). Besides the empirical studies, several theoretical works have also explicitly integrated habitat quality into metapopulation models because of its importance on species persistence (North and Ovaskainen, 2007; Hodgson et al., 2009; Visconti and Elkin, 2009; Hiebeler et al., 2013), and even both spatial and temporal dynamics of habitat quality have been included (DeWoody et al., 2005). However, these studies have generally considered dynamics between patches, while ignoring within-patch spatial dynamics. Furthermore, we still lack the systematic investigation of the spatial effects on species persistence resulting from the clustering of varying-quality habitat patches (see review by Mortelliti et al., 2010).

We adopted a pair approximation (PA) method to integrate habitat quality and landscape heterogeneity. This method incorporates local spatial correlations between adjacent sites on a lattice (Matsuda et al., 1992). The technique has increasingly been recognised as a valuable tool for characterising nearest-neighbour interactions in homogeneous or fragmented landscapes (e.g., Harada and Iwasa, 1994, 1996; Hiebeler, 2000; Ovaskainen et al., 2002), because it allows spatially realistic models to be analysed and understood more thoroughly than spatially explicit cellular automaton (CA) simulations (e.g., Hiebeler, 2000; Ovaskainen et al., 2002). Using the Hiebeler (2000, 2007) landscape generation algorithm, we first produced the heterogeneous landscapes, with two different-quality habitats of varying spatial arrangement (i.e., habitat clumping). Next, we constructed PA models to simulate species persistence in homogeneous versus heterogeneous landscapes. Because habitat quality obviously influences species birth and/or death, in the interests of model simplicity, here we represented habitat quality by species mortality rate. Compared to the PA models mentioned above, the PA model developed here is more complex because heterogeneous landscapes are considered to have two habitats of different suitabilities for species survival. Finally, we applied

spatially realistic CA simulations to determine how accurately PA could model the population dynamics. Using these models, we explored how dispersal traits (i.e., local or global dispersal) and density dependence modulate the effect of habitat quality and arrangement on species persistence and extinction thresholds.

## 2. Model description

### 2.1. Heterogeneous landscape generation

A square lattice of size  $L \times L = 100 \times 100$  cells ( $L$  is the length of the lattice) was generated to simulate a landscape, which acted like a torus to avoid edge effects (also applicable to homogeneous landscapes). Each cell (i.e., site) can be either empty or occupied by an individual. To introduce habitat arrangement (i.e., fragmentation or clumping), we defined a heterogeneous landscape to consist of two different-quality sites  $E_1$  and  $E_2$ , where the  $E_1$ -sites (global density  $\rho_{E_1} \in [0,1]$ ) were assumed to be more suitable for species survival than  $E_2$ -sites (global density  $\rho_{E_2} \in [0,1]$ ); note that  $\rho_{E_1} + \rho_{E_2} = 1$ . The clumping degree of a given habitat (either  $E_1$  or  $E_2$ ) was expressed by the local density  $q_{iji} = \rho_{ii}/\rho_i$  with  $i \in \{E_1, E_2\}$  (Matsuda et al., 1992), where  $q_{iji}$  ( $0 < q_{iji} < 1$ ) was the conditional probability of the nearest neighbour of an  $i$ -site also being an  $i$ -site (von Neumann neighbourhood with four neighbours for each site), and the pair density  $\rho_{ii}$  (i.e., doublet density) represented the probability when choosing a pair of nearest neighbours randomly that both of them are  $i$ -sites.

Following the landscape generation algorithm for two habitats (Hiebeler, 2000, 2007), the range of habitat clumping for a given habitat  $E_2$  is

$$(2 - 1/\rho_{E_2}) < q_{E_2/E_2} < 1, \tag{1}$$

so the allowable clumping degree of a given habitat depends on its global density.

Using Hiebeler's landscape algorithm (Hiebeler, 2000, 2007), we show the typical landscape configurations of varying habitat clumping ( $q_{E_2/E_2}$ ) at  $\rho_{E_2} = 0.5$  (Fig. 1). In the special case of  $\rho_{E_2} = q_{E_2/E_2}$  (case II), both habitats ( $E_1$  and  $E_2$ ) are randomly distributed, while the cases of  $\rho_{E_2} > q_{E_2/E_2}$  (case I) and  $\rho_{E_2} < q_{E_2/E_2}$  (case III) respectively represent the over-dispersed (high fragmentation) and clumping (low fragmentation) patterns of two habitats. As this approach is able to differentiate habitat clumping (e.g.,  $q_{E_2/E_2}$ ) from habitat amount (e.g.,  $\rho_{E_2}$ ), it provides a convenient method to separately study their effects on species persistence.

### 2.2. Spatially structured population in homogeneous landscapes

In this section we model species persistence in a homogeneous landscape with only one type of habitat  $E$ , where each site can be either occupied by an individual (indicated by  $I$ ) or vacant ( $E$ ). For simplicity, two extreme types of dispersal – local and global – are included in the model, with local dispersal limited to nearest neighbours (i.e., clonal growth) and global dispersal being random across the entire landscape (i.e., long-range seed dispersal).

In the model, species death is influenced by both intrinsic mortality and density dependence, while births are generated by local or global dispersal. As with the previous PA models structured by Harada and Iwasa (1994, 1996), the dynamics of global density  $\rho_I$  can be denoted as

$$\frac{d\rho_I}{dt} = \underbrace{-(d + \gamma \cdot q_{I/I}) \cdot \rho_I}_{\text{Intrinsic mortality + Density dependence}} + \underbrace{\alpha \cdot \rho_I \cdot (1 - q_{I/I})}_{\text{Local dispersal}} + \underbrace{\beta \cdot \rho_I \cdot (1 - \rho_I)}_{\text{Global dispersal}}, \tag{2}$$

where  $d$  is the intrinsic mortality rate, and  $\gamma \cdot q_{I/I}$  indicates enhanced mortality caused by the presence of neighbours, namely

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