The effects of clonal integration on the responses of plant species to habitat loss and habitat fragmentation

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ABSTRACT

Exploring the mechanism of plant species persistence in fragmented landscapes has already become a major issue in spatial ecology. Most of previous models predicted that habitat loss and fragmentation negatively impact plant species persistence, while empirical studies found diverse responses of plant species to habitat fragmentation, suggesting that some critical process may be overlooked in these models. Clonal species has the ability to well explore the resources under habitat fragmentation via clonal integration. However, responses of such species to habitat fragmentation have rarely been considered, especially in the aforementioned models. Here we developed a pair approximation model by considering clonal integration to explore the underlying mechanism of species' diverse responses to habitat fragmentation. The persistence of global dispersers (i.e. species with seed reproduction) depends on habitat loss not habitat fragmentation, whereas the persistence of local dispersers (i.e. species with clonal reproduction) or mixed dispersers (i.e. species with both seed and clonal reproduction) is influenced by both habitat loss and habitat fragmentation. Furthermore, habitat fragmentation shows diverse effects (i.e., positive, neutral or negative effects) on the persistence of local dispersers or mixed dispersers via clonal integration. Our results provide theoretical guidance for species conservation, which highlights the crucial role of species' ecological traits in response to habitat loss and fragmentation.

1. Introduction

Habitat destruction, including two extreme forms (habitat loss and habitat fragmentation), is one of the main drivers of biodiversity loss (Wilcox and Murphy, 1985; Tilman et al., 1994; Liao et al., 2017a,b,c). Exploring the underlying mechanism of species persistence under habitat destruction has consequently become a critical topic in biodiversity conservation (Dytham, 1995; Fahrig, 2003; Bruggeman et al., 2010; Heinrichs et al., 2016). Habitat loss refers to the reduction of habitat availability, and habitat fragmentation reflects the configurational fragmentation of the remaining habitat (Liao et al., 2013a,b). Numerical studies have theoretically investigated the impacts of habitat loss and/or habitat fragmentation on plant population dynamics (Bender et al., 1998; Hiebeler, 2000, 2007; Liao et al., 2013a, 2016a,b). A critical species extinction threshold of habitat loss was found, above which a species cannot persist anymore and it will go extinct (Bascompte, 2003). Moreover, to maintain species persistence at high levels of habitat fragmentation, more suitable habitats are needed, and vice versa when suitable habitats are clustered (i.e., low level of habitat fragmentation). However, contrary to predictions from most of previous

modelling, some recent studies have found that habitat fragmentation can both negatively and positively affect species survival (Dufour and Buttler, 2006; Alofs and Fowler, 2010; Fahrig, 2017; Liao et al., 2017c). Such contradictory findings suggest that some crucial process may be overlooked in previous models.

In natural condition, clonal plant species firstly exploit resources, and then redistribute energy or resources between parental genets and ramets through connections, such as rhizome and stolon (Alpert and Mooney, 1986; Wijesinghe and Handel, 1994; Pennings and Callaway, 2000). Such process of reallocation resources is known as clonal integration, which allows some ramets to grow on resource-low sites to survive by receiving resources from the interconnected ramets that growing on resource-rich sites (Stuefer et al., 1994; Price and Marshall, 1999; Oborny et al., 2000). Clonal plant species tend to be better competitors on fragmented landscapes. For example, comparing with clonal plant species, on fragmented landscapes short-lived and non-clonal plant species went extinct faster since they were more susceptible to habitat loss and isolation (Lindborg, 2007; Lindborg and Pärtel, 2012). Therefore, we conjecture clonal integration may be one of the important processes that have been ignored in the abovementioned

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models.

Our previous study found that different reproduction modes of plant species can affect their performances in the lattice habitat by analysing the pair approximation (Ying et al., 2014). Here we extend our pair approximation model by taking the process of clonal integration into account. Then we simulate the responses of different plant species to habitat loss and habitat fragmentation. Hence, habitat loss and habitat fragmentation are expected to influence the persistence of clonal species differently (i.e., positive, neutral or negative), which greatly depend on their reproduction modes (sexual or asexual reproduction) as well as the clonal integration.

2. Method

2.1. Model assumptions

To simplify, a plant species is assumed to grow on an ideal landscape, which includes two types of habitats, i.e., suitable and unsuitable, denoted as S and U, respectively. Only the S-sites are able to be colonized by plants. Each habitat site only has one status, either empty (denoted as 0) or occupied by a plant individual (denoted as 1). Collectively, there are four cases considering the types of habitat and the statue of the habitat: suitable and empty (denoted as S_0), suitable and occupied (denoted as S_1), unsuitable and empty (denoted as U_0), and unsuitable and occupied (denoted as U_1). All individuals are assumed to be genetically identical. Each individual can propagate by sexual reproduction and/or by asexual reproduction, where the former mainly refers to seed reproduction with long-range dispersal via animals, wind, or water (global dispersal, Ran, 2006; He et al., 2009), while the latter reflects that plants reproduce offspring (e.g., rhizome and stolon) through clonal growth with distance-limited extension (local dispersal, Santamaría, 2002; Silvertown, 2008). In our case, clonal plants are assumed to have the ability to randomly propagate in any empty site via sexual reproduction or to the nearest neighboring sites via asexual reproduction. Each site has a few (z) nearest neighboring sites, in our case $z = 4$ (adopting von Neumann neighbourship from Lohn and Reggia, 2002). Moreover, we assume that the offspring reproduced via sexual reproduction can only survive in suitable sites, while the offspring reproduced via clonal growth can survive in both suitable and unsuitable sites due to clonal integration.

2.2. Landscape patterns

The landscape pattern in our case is described by using the total density of S-sites in the landscape (p_S), and the clumping degree of S-sites ($q_{S/S}$) (Matsuda et al., 1992). The $q_{S/S}$ is defined as the probability that the neighbour of an S-site is also an S-site, i.e., $q_{S/S} = p_{SS}/p_S$, where the pair density p_{SS} is the probability that a randomly chosen pair of neighbouring sites are both S-sites. It is clear that the degree of habitat loss can be described by $p_U = 1 - p_S$ (i.e., total density of U-sites). While the fragmented parameter $q_{U/S} = 1 - q_{S/S}$ can be used to describe the habitat fragmentation since the clumping degree of S-sites ($q_{S/S}$) is a measurement of the aggregation of S-sites (i.e., the average fragment size). The maximum possible degree of habitat fragmentation is constrained by habitat loss (Hiebeler, 2000, 2007, Liao et al., 2017a,b,c).

$$q_{U/S} \leq p_U/(1-p_U) \tag{1}$$

Different values of the parameters p_U and $q_{U/S}$ can generate various fragmented landscapes (Hiebeler, 2000, 2007) (Fig. 1). If $p_U = q_{U/S}$, the unsuitable habitats are randomly distributed in the landscape (Fig. 1a); while $p_U < q_{U/S}$ and $p_U > q_{U/S}$ represent the over-dispersal (i.e., high fragmented) patterns (Fig. 1b) and clustered (or low fragmented) patterns (Fig. 1c and d), respectively. In the following simulations, the dynamic model of clonal plant species on destructive landscapes is investigated for landscapes with varying values of the parameters p_U and $q_{U/S}$.
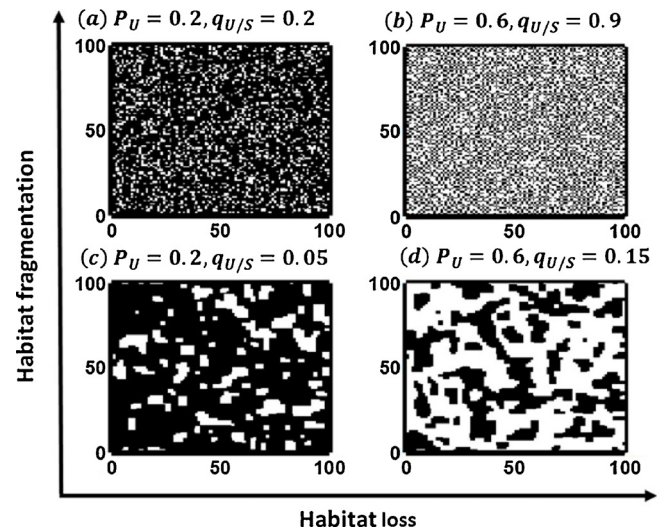

Fig. 1. Fragmented landscapes under different cases of habitat loss (p_U) and fragmentation ($q_{U/S}$). Unsuitable and suitable habitats are indicated by white and black, respectively.

2.3. Modelling species persistence in fragmented landscapes

The dynamics of clonal plant species in fragmented landscapes can be described as:

$$\frac{dp_{S_1}}{dt} = \underbrace{(c_1 \bullet q_{S_1/S_0} + c_2 \bullet q_{U_1/S_0}) \bullet p_{S_0}}_{clonal\ reproduction} + \underbrace{(s_1 \bullet p_{S_1} + s_2 \bullet p_{U_1}) \bullet p_{S_0}}_{seed\ reproduction} - \underbrace{d_1 \bullet p_{S_1}}_{mortality} \tag{2a}$$

$$\frac{dp_{U_1}}{dt} = \underbrace{c_1 \bullet q_{S_1/U_0} \bullet p_{U_0}}_{clonal\ reproduction} - \underbrace{d_2 \bullet p_{U_1}}_{mortality} \tag{2b}$$

where p_{S_1} and p_{U_1} denote the frequency of S_1-sites and U_1-sites in the whole lattice landscape, respectively, and other parameters are summarized in Table 1.

Eq. (2a) describes the dynamic of clonal plants' density in the suitable sites (p_{S_1}). The density of clonal plants in the suitable habitats is influenced by the ecological processes (i.e., clonal reproduction, seed reproduction and mortality). The S_0-sites can transfer to S_1-sites via clonal reproduction from its neighboring parental plant in the suitable site ($c_1 \bullet q_{S_1/S_0}$) or in the unsuitable site ($c_2 \bullet q_{U_1/S_0}$) with local dispersal, or via seed reproduction of the clonal plants in the suitable habitat ($s_1 \bullet p_{S_1}$) or in the unsuitable habitat ($s_2 \bullet p_{U_1}$) with randomly global

Table 1
Parameters and their definitions.

Variables and parameters	Definitions
p_i	The global density, i.e., the frequency of i sites in the whole lattice landscape ($i = S_1, S_0, U_1, U_0, S, U$).
p_{ij}	The global pair density, i.e., the frequency of the neighboring pair ij sites ($i = S_1, S_0, U_1, U_0, S, U$).
$q_{i/j}$	The local density, i.e., the conditional probability of i sites among the nearest neighbors of a randomly chosen j site ($i, j = S_1, S_0, U_1, U_0, S, U$).
$q_{i/jk}$	The local density, i.e., the conditional probability that a randomly chosen neighbor of the j site in the pair jk site is an i site ($i, j, k = S_1, S_0, U_1, U_0, S, U$).
c_1	The clonal reproductive rate of individuals in suitable sites
c_2	The clonal reproductive rate of individuals in unsuitable sites
s_1	The seed reproductive rate of individuals in suitable sites
s_2	The seed reproductive rate of individuals in unsuitable sites
d_1	The mortality rate of individuals in suitable sites
d_2	The mortality rate of individuals in unsuitable sites