# Patch dynamics of various plant-animal interactions in fragmented landscapes

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ABSTRACT

Habitat destruction, characterized by patch loss and patch fragmentation, has been recognized as one of leading factors driving species loss. Although some studies have already explored how patch loss affects metacommunity dynamics, the effect of patch configurational fragmentation remains vaguely understood. Here we construct a patch-dynamic model for various plant-animal interactions in fragmented landscapes, including neutralism (0, 0), poison (0, −), competition (−, −), predation (−, +), fruitivory (0, +) and mutualism (+, +). Counter-intuitively, negative plant-animal interactions (harmful for one or both species) show stronger tolerance to habitat destruction (i.e., higher species persistence) than positive interactions (beneficial to one or both species), in spite of lower patch occupancy. This is because animal species survival in positive interactions largely depends on plant species abundance. Furthermore, neutralism displays most robust to both patch loss and fragmentation while mutualism showing most vulnerability. Essentially, neutral interaction leads to more patches available for both plant and animal species, while in mutualistic interaction (e.g., pollination), both plant and animal species can only persist when they co-occur at the same patches. Compared to other interactions, predation (−, +) results in lowest patch occupancy, but such trophic interaction does not exhibit highest sensitivity to habitat destruction. Overall, our modelling framework provides new insights into how different plant-animal interactions respond to landscape fragmentation.

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## 1. Introduction

Natural disturbances (e.g., fire, drought and flood) and anthropogenic activities (e.g., deforestation and land use change) result in habitat destruction, thereby speeding up species extinction (Ehrlich, 1995; Thomas and Morris, 1995; Fahrig, 2001). Thus, exploring the effect of habitat destruction on species persistence and diversity maintenance has attracted more and more attentions from ecologists. In the past decades, based on niche theory (Hutchinson, 1959; Weiher and Keddy, 1999; Wright, 2002; Chase and Leibold, 2003; Silvertown, 2004), a complete set of species-abundance differential equations has been established by using Lotka-Volterra model (Lotka, 1910; Volterra, 1926), deriving the relationship between species abundances and habitat loss in a metacommunity. For example, classical metacommunity theory

has been utilized to explore how species occupancy responds to patch loss in a food chain (Pillai et al., 2010). In addition, Fortuna and Bascompte (2006) performed simulations on a mutualistic plant-animal system, obtaining the parameter region of species persistence as well as the threshold of habitat loss where the community collapses.

According to Fahrig (2002, 2003) and Liao et al. (2013a,b, 2016a; Liao et al., 2017a,b,c), habitat destruction induces two extreme consequences: patch loss and patch fragmentation, where the former is the loss of available patches, while the latter refers to the spatial arrangement of the remaining habitat patches. Recently, some modelling studies have started investigating the effects of patch loss on species persistence based on the classic metapopulation models (e.g., Bascompte and Solé, 1998; Hanski, 1998; Melián and Bascompte, 2002; Kondoh, 2003). Most of these studies concluded that patch loss can reduce population sizes and therefore species extinction. However, these studies largely ignored the impact of spatial habitat fragmentation because of configurational complexity (e.g., Venier and Fahrig, 1996; Fortuna and Bascompte, 2006;

Pillai et al., 2010), which has already been proven experimentally to affect species persistence (Carrara et al., 2014; Martinson and Fagan, 2014; Burgett and Chase, 2015). Thus, it is necessary to further study how habitat configurational fragmentation affects species coexistence in plant-animal interaction systems.

There are some researches assuming that species may have local (Eriksson, 1989; Liao et al., 2013a,b; Fukui and Araki, 2014) or global dispersal (Cain et al., 2000; Nathan et al., 2008; McConkey et al., 2012). Local dispersers are only able to colonize the neighbouring suitable patches, while global dispersers are assumed to establish in any suitable patch randomly across the entire landscape (Hiebeler 2000, 2007; Liao et al., 2013a,b, 2016a,b, 2017a,b,c). Several single population models have concluded that patch fragmentation strongly impedes the growth of distance-limited dispersers, while long-range dispersers are much less influenced (Johst and Drechsler, 2003; Kallimanis et al., 2006; Liao et al., 2013a,b, 2016a). As a consequence, species dispersal strategy (e.g., local and global) should be considered in plant-animal interactions, as plant species in most cases can only disperse within a shorter range than animal populations.

In order to characterize habitat fragmentation and local neighbouring dispersal, the pair approximation technique (PA) has been used to describe the neighbouring correlation (Harada and Iwasa, 1994; Liao et al., 2016b). Using PA approach, Hiebeler (2000, 2007) found in a fragmented landscape, not only habitat loss but also habitat fragmentation can have a significant influence on species persistence. Furthermore, Liao et al. (2016a) recently performed an extension of patch-dynamic model on a food chain in fragmented landscapes, finding that long-range dispersers at higher trophic levels display more sensitivity to habitat loss and fragmentation due to a trophic cascade. Using the PA method to characterize spatial patch clustering degree and local dispersal approximately, such extended patch-dynamic model allows one to explore the separate effects of patch loss and fragmentation. Despite the approximations, this model can yield qualitatively similar results as more realistic spatially explicit simulations (Liao et al., 2016a), thus it can be further applied to other types of interactions, such as competition, mutualism (e.g., pollination) and facilitation.

Here we stress that besides predation (−, +) between plants and animals, there also exist other plant-animal interactions, such as mutualism (+, +) (e.g., pollination), neutralism (0, 0) (i.e., no interaction), poison (0, −) (i.e., nepenthes and insect), competition (−, −) and fruitivory (0, +). Therefore, we use an extended patch-dynamic modeling framework developed by Liao et al. (2016a) to describe the above six plant-animal interactions in fragmented landscapes, so as to explore how patch loss and fragmentation separately and interactively affect different plant-animal interactions and which interaction is most robust to habitat destruction.

## 2. Methods

### 2.1. Landscape structure

Similar to Liao et al. (2016a), we assume the landscape includes two types of habitat patch: unsuitable ($U$) and suitable ($S$), where $U$-patches ($U$-patch loss) are unsuitable for any species establishment, while $S$-patches is suitable for species colonization. The clustering degree for a given patch (for example $S$) can be described by patch connectivity $q_{S/S} = \rho_{SS}/S$, in which the pair density $\rho_{SS}$ denotes the probability that a randomly chosen pair of neighboring patches both are suitable. Thus patch connectivity (so-called patch clustering degree) $q_{S/S}$ is the conditional probability that the neighbor of a target $S$-patch is also an $S$-patch. Here we adopt the von Neumann neighborhood with each patch having four orthogonally adjacent patches ($z = 4$). The fragmentation degree of $S$-patches is negatively

**Table 1**
Parameter interpretations.

| Parameter | Interpretation |
|-----------|----------------|
| $U$ | Fraction of unsuitable patches (i.e., patch loss) |
| $S$ | Fraction of suitable patches (i.e., patch availability) |
| $P$ | Fraction of suitable patches occupied by plant species |
| $A$ | Fraction of suitable patches occupied by animal species |
| $\rho_{ij}$ | Probability of a randomly chosen pair of neighboring patches that one patch is $i$ and the other is $j$ |
| $q_{i/j}$ | Conditional probability that the neighbor of a target $j$-patch is an $i$-patch |
| $q_{S/S}$ | Clustering degree of suitable patches |
| $C_i$ | Colonization rate of specie $i$ |
| $e_i$ | Extinction rate of specie $i$ |
| $\mu_{ij}$ | Increased extinction rate of species $i$ because of species $i$-$j$ interaction |

related to their clustering degree, defined as $1-q_{S/S}$. Based on the orthogonal neighboring correlation method of landscape generation (Hiebeler 2000, 2007), we have

$$2 - 1/S < q_{S/S} < 1. \qquad (1)$$

### 2.2. Patch-dynamic models of various plant-animal interactions

In a fragmented landscape where each suitable patch can be empty or occupied by either plant ($P$) or animal ($A$), we assume plant species have local neighbouring dispersal (local dispersal), while animal species can disperse globally across the landscape (global dispersal). As such, plant species can only colonize the neighbouring unoccupied $S$-patches, while animal species can establish in any unoccupied suitable patches in the whole landscape.

Similar to Liao et al. (2016a), we can derive the patch dynamics for plant-animal system without interactions (i.e., neutralism) as

$$\begin{cases} \dfrac{dP}{dt} = \underbrace{C_P(P - \rho_{PP} - \rho_{PU})}_{\text{Local dispersal}} - \underbrace{e_P P}_{\text{Extinction}} \\ \dfrac{dA}{dt} = \underbrace{C_A A(S - A)}_{\text{Global dispersal}} - \underbrace{e_A A}_{\text{Extinction}} \end{cases}. \qquad (2)$$

All parameters are defined in Table 1. In Eq. (2), the dynamics for both plant and animal include two terms: species colonization and extinction. The factor $P - \rho_{PP} - \rho_{PU}$ denotes the probability that a vacant $S$-patch neighbors a randomly chosen $P$-patch (i.e., occupied by plant), as there exist three possible neighbour states for a target $P$-patch: $P, U, s$ (unoccupied suitable patches), and plant species can only colonize the unoccupied neighbouring $s$-patches (see more details in Liao et al., 2016a). Since the terms $\rho_{PP}$ and $\rho_{PU}$ change over time, we further describe their transition rates in Appendix A in Supplementary material to construct the closed system. The factor ($S$-$A$) is the proportion of suitable patches unoccupied by animal species.

For poison (0,-), we assume animal species may mistakenly eat the poisonous leaf of plant species, and then would go to die immediately. Similarly, the patch dynamics of plant population include two terms: colonization via neighbouring dispersal and intrinsic extinction. Yet, the dynamics of animal populations consist of three parts: colonization via global dispersal, intrinsic extinction and additional extinction rate by mistakenly eating poisonous plant leaves. Therefore, we have

$$\begin{cases} \dfrac{dP}{dt} = \underbrace{C_P(P - \rho_{PP} - \rho_{PU})}_{\text{Local dispersal}} - \underbrace{e_P P}_{\text{Extinction}} \\ \dfrac{dA}{dt} = \underbrace{C_A A(S - A)}_{\text{Global dispersal}} - \underbrace{e_A A}_{\text{Extinction}} - \underbrace{\mu_{AP} PA}_{\text{Poison}} \end{cases}. \qquad (3)$$