



Frugivory and seed dispersal: Extended bi-stable persistence and reduced clustering of plants

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ABSTRACT

Frugivores and fleshy-fruited plants commonly engage in the mutually beneficial interaction by dispersing seeds while consuming fruit pulps. Such mutualistic interactions can have profound impacts on the persistence and distributions of plant populations. Based on pair approximation, we here develop a process-based mechanistic model that captures the dynamics of the mean and local densities of plants and the density of animals. The model considers three components of frugivory: the strength of frugivore-plant mutualistic interaction, the efficiency of seed dispersers, and the germination probability of seeds. Results show that seed dispersal by animals is crucial to the extended persistence of plants by reducing the level of aggregation and thus local intraspecific competition. Importantly, frugivory can only be beneficial to the plants if the animal is an efficient seed disperser with limited risks/costs of dispersal plus adequate number of encounters. Otherwise, frugivory could become a main driver of plant extinction from seed predation by the animals. In conclusion, frugivorous seed dispersal could allow persistence of plants in habitats that otherwise require much higher levels of fecundity and dispersal rate to survive. Such extended persistence highlights the threshold phenomenon in plant conservation – extended persistence in environments that are difficult to restore once the plants have collapsed.

1. Introduction

Seed dispersal is the movement of seeds away from the parental plants, which plays a crucial role in regulating the distribution of seeds, seedlings and adult plants (Nathan and Muller-Landau, 2000; Beckman et al., 2012) and is therefore crucial to plant demography and diversity (Howe, 1984; Herrera, 1989, 2002; Stoner and Henry, 2009; Traveset et al., 2013). Seeds that are dispersed by vectors such as animals are often encapsulated in fleshy fruits to lure animal dispersers (Herrera et al., 2002; Perez-Mendez et al., 2015), and the interaction between fleshy-fruited plants and animals is of mutualistic kind, benefiting both partners (Herrera et al., 2002; Schleuning et al., 2011). In fact, through frugivorous seed-dispersal, plants can drastically reduce intraspecific competition for resources, inbreeding pressure and density-dependent seed mortality near parental plants (Howe and Smallwood, 1982; Herrera et al., 2002), while frugivores obviously gain nutrients from consuming fruit pulps.

The number, quality and size of fruits are such to entice more visitors and maximize visiting frequencies: evidence supports increased visits and thus dispersed seeds when more fruits are available (Howe

and Estabrook, 1977; Schleuning et al., 2011). However, the number of consumed fruits per visit depends on the body mass of the frugivore (Jordano, 2000). Thus, plant-frugivore interactions strongly rely on size matching (Donoso et al., 2017): large fruits are usually eaten by mammals, whereas smaller fruits by birds due to limits to gape size. As a result, fruit size is strongly related with the mobility of their animal consumers (Jordano et al., 2007). Efficient seed dispersers can disperse large number of seeds to a suitable and less competitive environment, where seeds can germinate with relatively low risks (Mokotjomela et al., 2016). Besides the usual risks associated with the fate of a dispersed seed (e.g. local density of adult plants and landing in unsuitable habitats; Caughlin et al., 2015; Howe, 1984; Beckman and Rogers, 2013), animal-dispersed seeds also face additional risks for obvious reasons (Janzen, 1970; Jordano, 2000): seeds can be damaged during handling, ingestion and digestion (Janzen, 1971; Herrera et al., 2002; Howe and Estabrook, 1977; Howe, 1984). Consequently, only a small fraction of eaten seeds can be dispersed and deposited into suitable habitats for germination and establishment (Nathan and Muller-Landau, 2000; Heleno et al., 2011). Effective frugivorous seed-dispersal thus requires a fine balance between benefits and risks to ensure the

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viability of plant populations.

In tropical regions, approximately 90% of fleshy-fruited plant species almost entirely depend on frugivores vertebrates for seed dispersal (Chama et al., 2013), whereas frugivorous vertebrates rely on fleshy-fruited plants as source of additional nutrients (Howe, 1984), often spending a significant portion of time handling fruits (Schleuning et al., 2011). Thus, the relationship between plants and their seed-dispersers is relatively strong (Jordano, 2000; Herrera et al., 2002; Alcantara and Rey, 2003; Perez-Mendez et al., 2015). For this reason, the loss of frugivores from often illegal hunting in tropical regions could boost up the extinction risk of plants (Caughlin et al., 2015). On the other hand, frugivorous seed-dispersal has also been considered an important tool for ecosystem restoration and conservation planning (Ribeiro da Silva et al., 2015), and thus its role in proliferating the persistence and distributions of plants warrants investigations.

Most process-based models of seed dispersal only consider seed dispersal by wind (e.g., Levin and Muller-Landau, 2000; Schurr et al., 2005; Nathan et al., 2002, 2011). The influence of seed dispersal by animals on the dynamics and spatial structure of plant populations remains elusive (C ortes and Uriarte, 2013). Recent works on frugivorous seed-dispersal are largely based on simulations and data analyses from multivariate statistics (Soons and Bullock, 2008; Schleuning et al., 2011; Chama et al., 2013; Calvino-Cancela, 2004; Caughlin et al., 2015; Mokoijomela et al., 2016), with most ignoring the spatial structure of plants and consequently often leading to incorrect conclusions (Harada and Iwasa, 1994).

Here, we propose a process-based mechanistic and deterministic model of frugivore seed dispersal. In addition to classic approaches mainly focusing on average density, we also consider the local densities of plants (Harada and Iwasa, 1994). This allows a better description of the plant-frugivore interaction (Morales et al., 2013) and to explore its effects not only on plant density but also its spatial structure (Beckman and Rogers, 2013; Caughlin et al., 2015). To make the model realistic, we further consider three essential components of frugivorous seed dispersal, including the strength of the frugivore-plant mutualistic interaction (Schleuning et al., 2011), the efficiency of the seed disperser (Schupp 1993, Mokoijomela et al., 2016), as well as the germination probability of seeds (Chama et al., 2013, Calvino-Cancela 2004). Specifically, the interaction strength in our model is determined by species abundance, fruit production rate, and animal attack rate. Finally, the model considers the benefit to animals from the interaction with plants contributing to an increased animal density due to extra food resources. Using this simple model, we are able to systematically investigate how all different factors influencing animal-mediated seed dispersal, including fruit production rate, plant local dispersal ability, frugivore dispersal efficiency and frugivore attack rate, alone or in combinations, can affect the spatial and temporal dynamics of plants. We further discuss possible implications to predicting plant extinction for better conservation, as well as suggest possible intervention measures on the frugivore population and/or on the plant-frugivore interactions to allow plant persistence or restoration.

This paper provides the first endeavour of modelling plant-frugivore mutualistic interaction using more accurate methodology of pair approximation that allows the formulation of spatial structures. The model highlights the significant contribution of frugivores to often extended plant population viability. However, only efficient frugivorous species can support such conditional persistence of plants in environments that would otherwise require high fecundity and natural dispersal ability to sustain. Using this model, early intervention strategies for preventing plant extinction can be set up once the dispersal efficiency of frugivores is measured. This model can provide new insights for forest managers on the time to introduce new frugivore individuals for conserving or restoring plant populations especially for those with low fecundity and natural dispersal ability.

2. Model and method

2.1. Pair approximation model of plant dynamics

First, we briefly recall the methodology of pair approximation used to build our model. Pair approximation is a method for constructing a system of ordinary differential equations for both global and local densities of a given population. It assumes that the dynamics of focal individuals are affected by its direct neighbours (local density) and propagules from all the population (global density) (Matsuda et al., 1992; Harada and Iwasa, 1994). Pair approximation method neglects the effect of secondary or even higher-order neighbouring individuals (e.g. the neighbour of a neighbour) on the dynamics of the population. The simplicity of pair approximation allows us to formulate spatial dynamics in an analytic fashion (e.g. Hui and Li, 2004; Hui and Richardson, 2017). In contrast to pair approximation method, the typical mean-field approximation only considers the global density dynamics and neglects the effect of all local interactions between neighbours. Therefore, pair approximation provides more accurate, spatially structured predictions of the population dynamics than the mean-field approximation, at the cost of an extra variable (the local density) being included in describing the system dynamics. In particular, if the local density is greater than the global density, plants are clustered in space; equal local and global densities define the spatially random structure; lower local density than the global density indicates segregated distributions of plants in the landscape (Hui et al., 2006). More details about pair approximation method is found in Matsuda et al. (1992) and Harada and Iwasa (1994).

We first consider an infinitely large and regular lattice model for plant population dynamics without animal-mediated seed dispersal. Each lattice site is either occupied (+ site) by an individual plant or empty (0 site). It is assumed that the size of a lattice cell can only allow one individual plant to establish, that is, each site can only be occupied by a single individual plant at a time (see Fig. 1 for a schematic representation). Seeds produced by a focal plant in a site can only grow in the nearest-neighbouring sites if they are empty (Fig. 1). Let P_+ denote the probability (called the *global density*) that a randomly chosen lattice site is occupied by an individual plant, and let $P_0 = 1 - P_+$ denote the probability that a randomly chosen lattice site is empty. Since birth of a new individual plant is restricted by the availability of a vacant nearest-neighbouring site, we consider $q_{0|+}$ to be the conditional probability that the nearest-neighbouring site of a given occupied site is an empty site where a seed can germinate and become a new plant. By definition $q_{+|+} = 1 - q_{0|+}$, where $q_{+|+}$ is the conditional probability that the nearest-neighbouring site of a given occupied site is also an occupied site; that is, the *local density* of the plants. The local density $q_{+|+}$ when compared with the global density describes the spatial structure of the plant population. Pair approximation allows an explicit description of the dynamics of both the global density P_+ and the local density $q_{+|+}$ in terms of ordinary differential equations. Since birth of a new plant can only take place if a seed is landed in an empty site in the neighbourhood of a focal plant, the plant population growth is governed by the following equation

$$\dot{P}_+ = -dP_+ + b q_{0|+} P_+ = -dP_+ + b(1 - q_{+|+}) P_+ \quad (1)$$

where b and d are the birth and natural death rates of plants, respectively. In Eq. (1), the first term refers to the natural death of plants while the second term refers to the establishment of a new plant in an empty site from locally dispersed seeds of a neighbouring adult plant.

By definition, $q_{+|+} = P_{++}/P_+$, and time derivation gives $\dot{q}_{+|+} = -P_{++}\dot{P}_+/P_+^2 + \dot{P}_{++}/P_+$, where P_{++} is the probability that two randomly chosen neighbouring sites (a pair) are both occupied. To define the local density dynamics $\dot{q}_{+|+}$ the pair dynamics \dot{P}_{++} needs to be specified. This is given by

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