Distance-responsive predation is not necessary for the Janzen–Connell hypothesis

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ABSTRACT

The Janzen–Connell hypothesis states that tree diversity in tropical forests is maintained by specialist predators that are distance- or density-responsive (i.e. predators that reduce seed or seedling survival near adults of their hosts). Many empirical studies have investigated whether predators are distance-responsive; however, few studies have examined whether distance-responsiveness matters for how predators maintain tree diversity. Using a site-occupancy model, we show analytically that distance-responsive predators are actually less able to maintain diversity than specialist predators that are not distance-responsive. Generally, specialist predators maintain diversity because they become rare when their host's densities are low, reducing predation risk. However, if predators are distance-responsive, and most seeds cannot disperse away from these predators, then seed predation rates will remain high, even if predator density is low across the landscape. Consequently, a reduction in a host's population density may not lead to a significant reduction in seed and seedling predation. We show that habitat partitioning can cause recruitment to be highest near conspecific adults, even in the presence of distance-responsive predators, without any change in the effect that the predators have on coexistence (a result contrary to predictions of the Janzen–Connell hypothesis). Rather, specialist predators and habitat partitioning have additive effects on species coexistence in our model, i.e., neither mechanism alters the effect of the other one.

1. Introduction

The Janzen–Connell hypothesis is one of the dominant explanations for how tree diversity is maintained in tropical forests (Gilbert, 2005; Leigh et al., 2004; Wright, 2002). It states that diversity is maintained by specialist natural enemies that increase seed and seedling mortality near conspecific adults (Connell, 1971; Janzen, 1970). Janzen (1970) referred to such natural enemies as either distance-responsive predators (i.e., predators that are prevalent near conspecific adults) or density-responsive predators (i.e., predators that are prevalent in areas of high conspecific seed density). Models have shown that specialized distance-responsive predators can promote diversity (e.g., Armstrong, 1989; Leigh, 1982; Sedio and Ostling, 2013). However, models have also shown that specialized predators can promote coexistence, even if the predators are not distance-responsive (Grover, 1994). This mechanism, known as predator partitioning, simply requires that each tree has its own specialist or relatively specialized natural enemy (Chesson and Kuang, 2008; Grover, 1994). This finding raises the question, does being distance-responsive change the ability of predators to promote the coexistence of their hosts? Previous theoretical studies have found contradictory results: they suggest that distance-responsive predators are more able (Adler and Muller-Landau, 2005), less able (Muller-Landau and Adler, 2007; Murrell, 2010), or equally able (Bever et al., 1997) to promote coexistence when compared to predators that are not distance-responsive. Here, we analyze theoretically whether distance-responsiveness changes how specialist or relatively specialized predators affect tree coexistence, both directly and through interactions with habitat partitioning.

We analyze whether distance-responsive predators affect tree coexistence differently when the predators are not strict (monophagous) specialists. A core element of the Janzen–Connell hypothesis is that the predators are specialists (Connell, 1971; Janzen, 1970); however, most natural enemies lie on a continuum between strict specialists and strict generalists (Novotny and

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Basset, 2005). Theoretical research has shown that, distance-responsive or not, predators do not need to be strict specialists to promote coexistence (Bever et al., 1997; Chesson and Kuang, 2008; Sedio and Ostling, 2013). Rather, predators need only to be relative specialists, and harm each host species differently. However, it is not known whether the benefit of predator partitioning is more or less sensitive to the impact of partial specialization when predators are distance-responsive. A few recent studies have examined how enemy dispersal interacts with degree of specialization (Bever et al., 1997; Murrell, 2010); however, no clear trend has emerged.

We also analyze how distance-responsive predators affect tree coexistence through their interactions with habitat partitioning. Habitat partitioning occurs when different species grow differently because of spatially varying environmental factors (Chesson, 2000a). Predation and environmental variation often have interactive effects on coexistence (Chesson and Kuang, 2008, 2010; Holt, 1984; Kuang and Chesson, 2009; Mordecai, 2014). For example, a recent model showed that generalist pathogens could not promote coexistence in a stable environment, but did promote coexistence in a temporally variable environment (Mordecai, 2014). Many studies have suggested that both habitat partitioning and specialist natural enemies may be operating simultaneously in tropical forests (Freckleton and Lewis, 2006; Hubbell et al., 2001; Uriarte et al., 2004; Wright, 2002). Therefore, to fully understand how distance-responsive predators affect tree coexistence, it is important to consider their interactions with habitat partitioning.

Distance-responsive predators and habitat partitioning seem particularly likely to interact, because they are predicted to produce differing spatial patterns. Under the action of distance-responsive predators, we expect seed and seedling survival to be highest far from conspecific adults, because those plants have escaped from their predators (Connell, 1971; Janzen, 1970). Many have suggested that this pattern is critical for distance-responsive predators to promote coexistence (e.g., Bagchi et al., 2010; Condit et al., 1992; Hubbell, 1980), and a common method for testing the Janzen–Connell hypothesis is to compare seedling growth and survival near a conspecific adult to growth and survival far away (Comita et al., 2014; Hyatt et al., 2003). However, under habitat partitioning we expect seed and seedling survival to be highest near conspecific adults, because adults are likely to be in favorable habitat (Chesson, 2000a; Hastings, 1983). If habitat partitioning causes survival to be highest near conspecific adults, it is unknown how this would affect the impact of distance-responsive predators on tree coexistence.

In this paper, we study whether being distance-responsive affects the impact that specialist predators have on tree coexistence. We construct a model of forest dynamics, in which coexistence is promoted by predator partitioning and habitat partitioning. Unlike previous studies, which relied mainly on simulations, we use analytical techniques to quantify contributions to species coexistence from the various applicable mechanisms (Chesson, 1994, 2000a). This quantification is based on the growth rates of a population after perturbation to low density, and gives a functional form for how various parameters (e.g., predation rates, seed dispersal) interact, and how each contributes to tree coexistence. We address the following questions:

(a) Is predator partitioning more or less able to promote coexistence when the specialist predators are distance-responsive?
(b) Is the impact of predator partitioning more or less sensitive to the degree of predator specialization when predators are distance-responsive?
(c) Does habitat partitioning alter how specialist predators affect coexistence?
(d) Can distance-responsive predators maintain diversity if seedling performance is highest near conspecific adults (rather than heterospecific adults)?

2. Model outline and methods

We modeled a forest using a discrete-time site-occupancy model. Fig. 1 illustrates the model, Table 1 lists the variables, and Table 2 gives a list of terminology. Where applicable, we use the notation and terminology of Chesson (2000a). The forest contains a large of number of sites, X. Each site holds one adult tree. Here X is chosen to be large enough that stochastic fluctuations in population density at the landscape scale are small enough to be ignored. There are n tree species competing to capture vacant sites. During each time step, t, some fraction δ of the adult trees die. Dead trees create gaps in the canopy, which are filled by new adults by the following time step. The new adults come from the seeds that are dispersed into each site during that time step. Every time step, each adult produces seeds that are immediately dispersed to compete for open sites. The variable Y_j represents the number of seeds produced by an adult of species j, weighted by their relative site-capturing ability. Dispersal is modeled using global dispersal with local retention: a fraction $(1 - d)$ of an adult's seeds remain at the natal site, and the remaining d seeds are dispersed evenly across the landscape. This model of dispersal greatly simplifies calculations, yet, as we show below, it produces similar results to more complex, spatially-explicit models (e.g., Muller-Landau and Adler, 2007; Murrell, 2010), while facilitating their interpretation. We assume that there is no long-term seed bank, and seeds die if they cannot capture a site during the time step they are produced. We assume that an adult will still produce seeds during the time step that it dies, and so a seed can capture a site previously held by its parent.

Competition for sites is modeled using biased lottery competition (Chesson and Warner, 1981). Under biased lottery competition, the seed that succeeds in becoming the new adult at each site is determined by chance, with a bias toward stronger competitors. Here, competitive ability of a seed of species j at site x is given by the quantity $E_{xj}\left(1 - P_{xj}(t)\right)$, where E_{xj} and $P_{xj}(t)$ are the effects of habitat and specialist predators, as described below. The probability that a seed of species j captures a site x in the event of an adult's death is

$$P\left(\text{captures gap} \mid N_{x1}(t), \ldots, N_{xn}(t), E_{x1}, \ldots, E_{xn}\right)$$
$$= \frac{E_{xj}\left(1 - P_{xj}(t)\right)}{C_x(t)}, \tag{1}$$

where $C_x(t)$, the intensity of competition, is the sum of $E_{xj}\left(1 - P_{xj}(t)\right)$ across all seeds at x. It is given by the formula

$$C_x(t) = \sum_{j=1}^{n} \left((1 - d)\, N_{xj}(t) Y_j E_{xj} \left(1 - P_{xj}(t)\right) \right.$$
$$\left. +\ d\bar{N}_j(t) Y_j E_{xj} \left(1 - P_{xj}(t)\right) \right), \tag{2}$$

where $N_{xj}(t)$ is the number of adults of species j at site x at time t (and thus $N_{xj}(t) = 0$ or 1, since each site holds only one adult), and $\bar{N}_j(t)$ is the proportion of sites occupied by species j across the landscape. Here, the $(1-d)N_{xj}(t)$-term represents the contribution of seeds from the adult that previously occupied x, and the $d\bar{N}_j(t)$-term represents seeds that were dispersed to x.

Because we assumed that seeds grow into adults in one time step, we do not track the population dynamics of seeds, seedlings, and other sub-adults separately. Eq. (1) therefore does not distinguish between factors that occur at each stage: a seed predator that reduces the probability of recruitment by 10% is equivalent to a sapling parasite that reduces the probability of recruitment by 10%. Because they are equivalent, we describe the effect of predators and habitat on seeds and seedlings interchangeably.