

A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond

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Summary

1 Although, in nature, seed dispersal usually declines with distance from the source, seedling establishment patterns are highly variable. An increase in seed survival can lead to either hump-shaped (Janzen-Connell (J-C) pattern) or declining (Hubbell pattern) establishment with distance from seed source, but declining establishment can also be generated if survival decreases with distance (McCanny pattern). Pathogens and seed predators are considered to be major mortality agents structuring recruitment patterns, but it is unclear how well predation alone can explain variation in these patterns.

2 We introduce a simple mechanistic model showing that distance and density-dependent seed predation can generate all of the observed recruitment patterns. Our approach provides the first mathematical reconstruction of conceptual models previously considered to be based on contrasting underlying mechanisms. Three easily measurable quantities (the proportion of seeds escaping predation at the source, and the mean distance from the source of dispersed seeds and of predators' activity) can be used to test for consistency with the J-C pattern. The association between recruitment patterns and plant (dispersal) and animal (predation) characteristics is robust with respect to parameter values and various functional forms.

3 The model shows that the J-C pattern can occur only if the mean distance over which predators are active is lower than that over which seeds are dispersed, corresponding to a system with host-specific, or immobile, seed predators (often invertebrates) that are restricted to areas of high seed density near adult plants, and therefore selecting for longer dispersal distances of seeds.

4 The Hubbell pattern is generated by the model when dispersal and predation distances are of equivalent magnitudes. The McCanny pattern emerges if more generalized, or more mobile, seed predators (often vertebrates) are attracted to the adult trees but also tend to forage farther away, thereby selecting for short dispersal distances that generate high densities needed to satiate seed predators.

5 The model also predicts that the total number of seeds surviving predation is lowest at intermediate distances, suggesting that distance-dependent predation promotes either short or long dispersal distances, or both (dimorphism).

Key-words: dimorphism, Janzen-Connell model, minimal models, plant recruitment, predator satiation, seed survival

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Introduction

The processes involved in plant recruitment (and seed dispersal, survival and seedling establishment in particular) have been extensively studied to understand

both the critical role of early developmental stages in plant population dynamics (Harper 1977; Howe & Smallwood 1982; Schupp & Fuentes 1995; Nathan & Muller-Landau 2000), and their implications for the diversity of plant communities (Janzen 1970; Hubbell 1980; Harms *et al.* 2000). Studies of seed dispersal in numerous plant species consistently reveal a rapid decline in seed density with distance from the parent plants

(Harper 1977; Howe & Smallwood 1982; Willson 1993), but patterns of seed survival and the resulting establishment patterns are quite variable (McCanny & Cavers 1987; Condit *et al.* 1992; Hammond & Brown 1998; Nathan *et al.* 2000). Patterns of seed/seedling survival depend on several (and possibly interacting) factors, such as microhabitat variability (Willson 1988; Kadmon & Shmida 1990), intra- and interspecific competition (Barton 1993; Fowler 1995), and seedling herbivory (Connell 1971; Packer & Clay 2003). In particular, post-dispersal seed predation by insects, birds and rodents is frequently the major cause of plant mortality, and is thus a key process in plant recruitment (Janzen 1971; Cavers 1983; Louda 1989; Schupp 1990; Crawley 1992; Hulme 1993; Manson *et al.* 1998; Wenny 2000). Pre-dispersal seed predation can also affect recruitment patterns, through its effects on the total seed output, but here the general term 'seed predation' exclusively refers to post-dispersal seed predation.

The various plant recruitment patterns observed have been attributed to a wide variety of factors, their interactions, and their variation in time and space. From the search for more specific explanations emerged one of the most exciting and controversial debates in the history of plant ecology. The core of this debate was a thought-provoking paper published by Daniel Janzen in 1970. Janzen, pursuing an explanation for the maintenance of high tree diversity in tropical forests, suggested that in general we should expect relatively low recruitment near conspecific adults, and that this is likely to prevent over-dominance of the common species. He argued that, for a given number of seeds dispersed, the processes of seed dispersal and seed survival are distance-dependent, and in a consistent manner: dispersal decreases while survival increases with distance from the parent plant. He specified the attraction of distance- or density-responsive seed predators (in

the broad sense mentioned above, including pathogens and parasites) to adult plants as the mechanism responsible for the increase in seed survival with distance from the source. Although distance- and density-dependent seed predation may be viewed as alternative forces (e.g. Hutchings 1986), the two are strongly correlated (Harper 1977; Howe & Smallwood 1982; Willson 1993); thus their joint, rather than independent, effect on seed predators should be considered.

Janzen summarized his hypothesis with a simple graphical model (Fig. 1): recruit density is relatively low near adults despite high density of dispersed seeds, due to the strong effect of seed predators; it increases to a peak at a certain distance, and then decreases farther away because of the low seed densities at long distances from the source. Connell (1971) independently proposed a similar mechanism to explain tree diversity in tropical forests, but attributed most impact to seedling herbivores. Thus, this recruitment pattern is generally called the Janzen-Connell (J-C) pattern.

To characterize the spatial relationships between parent plants and recruits, we need to explore the variation in dispersal (defined here as the flux of seeds arriving at unit area per unit time prior to predation), survivorship (the probability of a seed escaping predation) and the resulting establishment (the density of surviving seeds at the end of the dispersal season). These three functions together constitute what can be called the parent-recruit distance pattern (here, simply, recruitment pattern). The J-C model (Fig. 1) is probably the best-known recruitment pattern; we call it the 'J-C pattern'. This pattern is sometimes incorrectly considered to be identical to the one emerging from the escape hypothesis (Howe & Smallwood 1982). This hypothesis, which refers to the increasing survival with distance for the source as a selective force for increasing dispersal distances, can also give rise to recruitment patterns

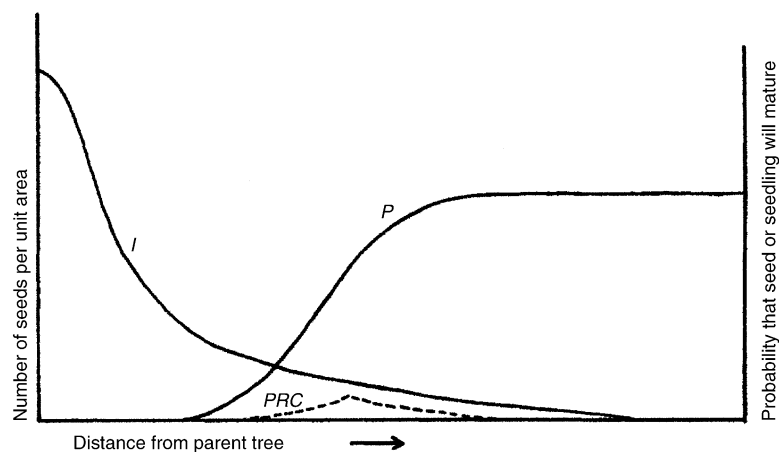


Fig. 1 The caption of the original graphical model of Janzen (1970, Fig. 1, p. 502) presented the following explanation: 'With increasing distance from the parent, the number of seeds per unit area (I) rapidly declines, but the probability P that a dispersed seed or seedling will be missed by the host-specific seed and seedling predators, before maturing, increases. The product of the I and P curves yields a population recruitment curve (PRC) with a peak at the distance from the parent where a new adult is most likely to appear'. [Reproduced with permission from Janzen, D. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.*, 104, 501–528, University of Chicago Press].

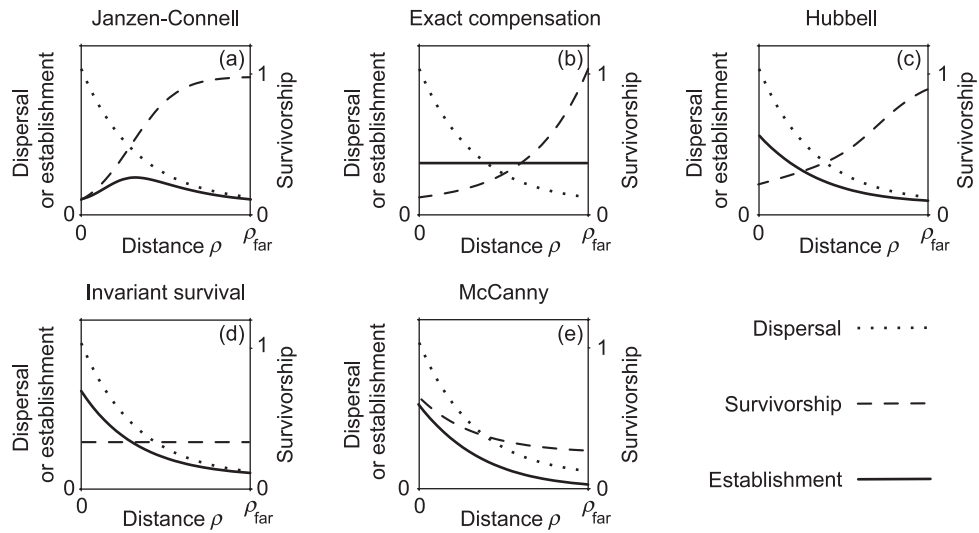


Fig. 2 McCanny's (1985) five alternative recruitment patterns represented as particular combinations of dispersal, survivorship and establishment curves: (a) J-C pattern; (b) exact compensation; (c) Hubbell pattern; (d) invariant survival; (e) McCanny pattern. McCanny's original exponential curves (linear in a semilog plot) were modified to avoid the paradoxical exponential increase in seed survival and to adhere more closely to observed patterns (not feasible for b).

other than the J-C pattern. For example, Hubbell (1980) predicted a monotonic decline in recruit density (hereafter the Hubbell pattern), arguing that seed densities are disproportionately high near adults, and that dispersal therefore decreases with distance faster than survival increases.

McCanny (1985) showed that the J-C and Hubbell patterns are just two out of five possible distinct types of recruitment patterns as summarized in Fig. 2 (see also McCanny & Cavers 1987). This important clarification received only limited attention (but see Houle 1995), perhaps because McCanny (following Hubbell 1980) restricted his approach to exponential curves. Exponentially increasing survivorship curves only make sense for a narrow range of distances near the parent plant, because their extension implies unrealistic (> 1) survival probabilities. One of McCanny's five recruitment patterns is exact compensation (Fig. 2b), which, similarly to the J-C (Fig. 2a) and the Hubbell (Fig. 2c) patterns, encompasses increasing survival with distance, hence corresponds to the escape hypothesis. However, this recruitment pattern cannot arise without such an exponential increase in survival. McCanny also included a case where survival decreases with distance (i.e. contrasting the escape hypothesis), which implies a rapid decline in recruit density (hereafter the McCanny pattern, Fig. 2e). Such inverse density-dependence seed mortality can be explained by predator satiation (Janzen 1971, 1976), when predators are satiated by the higher seed densities near adult plants (Augspurger & Kitajima 1992; Burkey 1994). Invariant survival (Fig. 2d) represents the transition between Hubbell and McCanny patterns.

In all cases dispersal declines with distance, but variation in survival leads to three qualitatively different basic types of recruitment patterns (J-C, Hubbell and

McCanny), and two potential transitional types (exact compensation and invariant survival). We emphasize that the term recruitment pattern refers to a particular combination of dispersal, survivorship and establishment curves, rather than the pattern described by the establishment curve alone (to avoid confusion we used establishment curve, rather than the commoner term recruitment curve, for the plot describing the number of surviving seeds as a function of the distance from the source). For example, the Hubbell, McCanny and invariant survival patterns embody establishment curves that are qualitatively similar: in all cases, establishment declines monotonically with distance. The recruitment patterns are, however, distinct because they result from survivorship curves that are qualitatively different: survivorship increases, declines or does not vary, respectively, with distance.

The ideas of Janzen and Connell have been continuously investigated over the past three decades, mostly empirically but also theoretically (see Hammond & Brown 1998 for review). A great deal of attention has been given to the community-level implications of their model (e.g. Condit *et al.* 1992; Wright 2002), but there has also been considerable work on the underlying mechanisms at the population level. Most of the empirical studies have been conducted in tropical forests (Hubbell 1980; Augspurger 1983; Clark & Clark 1984; Augspurger & Kitajima 1992; Schupp 1992; Howe 1993; Terborgh *et al.* 1993; Burkey 1994; Notman *et al.* 1996; Hammond & Brown 1998; Harms *et al.* 2000), while a few studies were conducted elsewhere (McCanny & Cavers 1987; Houle 1995; Manson *et al.* 1998; Nathan *et al.* 2000). Relatively few studies have, however, included data on all three curves (i.e. dispersal, survivorship and establishment) required to distinguish J-C from other recruitment patterns. Nevertheless, these few studies

were sufficient to provide empirical evidence that was consistent, in some situations, with the J-C (Augspurger 1983; Nathan *et al.* 2000; Wenny 2000), the Hubbell (Augspurger 1983; McCanny & Cavers 1987; Augspurger & Kitajima 1992) and the McCanny (McCanny & Cavers 1987; Augspurger & Kitajima 1992; Notman *et al.* 1996) or invariant survival (McCanny & Cavers 1987; Notman *et al.* 1996) patterns in others. Yet, despite this field evidence for the existence of various recruitment patterns, there is no agreement about their underlying mechanisms (Clark & Clark 1984; Hammond & Brown 1998). Previous studies (e.g. Hubbell 1980; McCanny 1985; McCanny & Cavers 1987; Burkey 1994; Manson *et al.* 1998) have considered the different recruitment patterns as competing alternatives, emerging from different mechanisms.

In this paper we introduce a simple dynamical model that couples seed dispersal and predation to describe the resulting spatial pattern of surviving seeds. Our focus on the effect of seed predation should not be misinterpreted as suggesting that other processes are not important determinants of plant recruitment patterns. Rather, we wish to explore, in a mechanistic way, whether variation in seed predation *alone* can lead to variable recruitment patterns, which components of predator activity are responsible for this variation and how. We emphasize that, following the original ideas of Janzen and Connell, seed predators and seedling herbivores are expected to behave in a similar manner and thus lead to similar outcomes; hence, the model presented here could be extended to account for seedling herbivory as well.

We explore the model behaviour by changing the values of some of its focal parameters (the number of dispersed seeds, the mean distances of dispersed seeds and of predators' activity) and examining their association with different recruitment patterns. We also examine the relationship between recruitment patterns and the cost of predation for plant reproductive success. Our main motivation in proposing this model is to encourage researchers to integrate theoretical and empirical studies of seed dispersal and predation for the enhanced understanding of plant recruitment processes. Towards this end, we keep the model simple with measurable and easily interpretable parameters. Unfortunately, while it is relatively easy to obtain data on dispersal (at the local scale on which the processes discussed in this paper typically operate), predation parameters of the model remain to be corroborated by field data. We therefore end this paper by suggesting ideas for empirical studies that could fill this gap and provide field data to test the model's predictions.

Materials and methods

MODELLING APPROACH

Models accounting for the formation of spatiotemporal patterns from any specific plant–animal interaction would require, in principle, a large number of variables

and parameters. For example, to model seed dispersal and predation, one may wish to include details on both plants (species composition, age structure and spatial arrangement) and their predators (foraging behaviour, alternate food resources and population or community dynamics). Other influential causes such as secondary and contagious dispersal or seed dormancy may also play an important role in shaping the observed plant recruitment patterns. However, to capture the essence of seed dynamics, we need to focus on the most important mechanisms, thereby keeping the number of variables and parameters as low as possible. A minimal model of this kind has a decisive advantage over more complex models because it provides the means to identify the key factors and interactions of a system, and how these factors determine the observed patterns. We use a minimal framework to explain how distance and density-dependent seed predation can give rise to various recruitment patterns observed in nature. Minimal models have proved successful in elucidating the fundamental dynamics of many complex ecological systems, including grazing (Noy-Meir 1975; Gatto & Rinaldi 1987), the impact of acidic deposition on vegetation (Gragnani *et al.* 1998), and forest fire regimes (Casagrandi & Rinaldi 1999).

A GENERAL MODEL

We consider a spatially isotropic case (i.e. with no preferred direction) in which seeds disperse from a point source (e.g. an isolated tree); for simplicity, we do not deal here with complexities caused by overlapping seed shadows (Ribbens *et al.* 1994; Clark *et al.* 1998; Nathan & Muller-Landau 2000). The area around the seed source is described using polar coordinates, with ρ and θ indicating, respectively, the distance from the source and the angle with a conventional zero.

However, because we assume isotropy, the angle from the source θ does not play any explicit role in our equations below. Thus, although the spatial setting we consider is two-dimensional, the equations are reduced to a single coordinate. We note that this is *not* equivalent to a spatial setting of a linear 1-m-wide transect departing from the seed source and extending to infinity. The dynamics of dispersed seeds is then described by a single state variable, $S = S(\rho, t)$, representing the density of seeds on the ground at distance ρ from the source and time t . Dispersal and predation are considered as continuous processes that take place throughout the dispersal season. This corresponds to the frequently observed progression of seed release over several weeks or months (Harper 1977; Howe & Smallwood 1982), with seed predation often occurring within a few days, or even minutes, after seed arrival (Hulme 1993; Wenny 2000). Our model aims to describe the overall spatial effect of seed predators, summarizing all their movements (i.e. those leading to seed consumption) in response to the expected seed distribution. The details of such movements vary in nature and may affect the resulting

seed predation; yet, from the perspective of plant recruitment, only the overall effect of predators matters. This approach helps to reduce complexity involved with spatially explicit description of animal movements, and still provides the means to characterize different predators, ranging from those strongly restricted to the vicinity of source plants, to those that prefer the vicinity of source plants but also forage farther away.

Our basic model is given by an ordinary differential equation, which describes the dynamics of dispersed seeds at a specific location as:

$$\frac{dS(\rho, t)}{dt} = \phi(\rho) - \omega(S(\rho, t)) - \eta(S(\rho, t), \rho) \quad \text{eqn 1}$$

where ϕ is the flux of arriving seeds, i.e. ϕdt is the density of dispersed seeds at distance ρ from the source during the infinitesimal time interval $(t, t + dt)$, ω is the instantaneous rate of seed loss resulting from all causes other than predation, and η is the loss due to predation. Equation 1 is thus a simple mass balance equation, with one input (the dispersal kernel ϕ) and two outputs (seed losses ω and η).

MODELLING SEED DISPERSAL

We describe the dispersal kernel as a temporally constant input during the dispersal season that decreases exponentially with distance from the source ρ :

$$\phi = \frac{2\alpha}{\pi D^2} \exp\left(-\frac{2\rho}{D}\right) \quad \text{eqn 2}$$

We choose the negative exponential over other functional forms such as Gaussian or fat-tailed kernels (Kot *et al.* 1996; Clark *et al.* 1998) because it generally fits observed seed shadows very well, for a variety of plant species and dispersal agents (Willson 1993; Nathan *et al.* 2000); note, however, that it does not account for complex seed shadows generated, for example, by specialized frugivores (Howe & Vandekerckhove 1979; Schupp *et al.* 2002). The two parameters α and D have important ecological meanings. The first (α) represents the total seed output, i.e. the total number of seeds dispersed from the source towards any direction per unit time:

$$\alpha = \int_0^{2\pi} d\theta \int_0^{\infty} \phi(\rho) \cdot \rho \cdot d\rho$$

For simplicity, we follow Clark *et al.* (1998) in using the term ‘fecundity’ for α ; it should be clarified, however, that α is rarely equal to seed production because it also incorporates all pre-dispersal seed losses, which can be substantial (Janzen 1971; Louda 1989; Crawley 1992; Ehrlén 1996). The second parameter (D) represents the mean distance travelled by dispersing seeds:

$$D = \frac{1}{\alpha} \int_0^{2\pi} d\theta \int_0^{\infty} \rho^2 \phi(\rho) d\rho$$

Figure 3 illustrates how α and D determine the shape of the dispersal kernel.

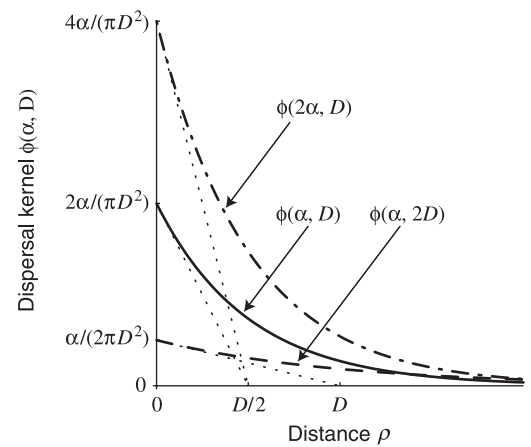


Fig. 3 Effects of varying the intensity (α) and distance (D) parameters of dispersal on the shape of the negative exponential dispersal kernel ϕ .

MODELLING SEED PREDATION

Our general model (1) distinguishes between seed loss due to predation (η) and seed loss due to all other causes (ω). We assume that ω is simply proportional to S through a constant mortality rate μ . Seed predation, instead, is described in greater detail, as the product of the predator density N and the per capita rate of seed intake $\psi(S)$, namely:

$$\eta = N\psi(S) \quad \text{eqn 3}$$

The quantity $\psi(S)$ is usually referred to as the ‘functional response’ of predators (Holling 1959). We choose a type II functional response (Holling 1959; Hassell 1978), because it has been recognized as most appropriate to describe plant–herbivore interactions (Noy-Meir 1975; Gatto & Rinaldi 1987). In particular, we use Holling’s disc equation:

$$\psi(S) = \frac{aS}{1 + aT_h S} \quad \text{eqn 4}$$

where T_h is the handling time and a is the searching rate, often called ‘instantaneous rate of discovery’ (Holling 1959) or the ‘searching efficiency’ of the predator (Hassell 1982). Through $\psi(S)$, our basic model thus incorporates density-dependent seed predation.

We incorporate negative distance-dependent predation by assuming that the response of predators to the variation in seed abundance is reflected in their numerical response (i.e. change in predator density). As stated by MacArthur (1972, p. 61), ‘[Predators] first decision – where to feed – is easy: the species should forage where the expectation of yield is greatest’. Thus, because seed dispersal always declines with the distance ρ from the parent plant, the density of seed predators is assumed to decline with ρ as well, and in a similar manner. Mathematically, this assumption differs from those of similar models (Solomon 1949; Holling 1959) in pertaining to distance rather than resource density, but is in accordance with Janzen’s (1970) emphasis that the

general mechanism shaping plant recruitment patterns is the attraction of seed predators to the vicinity of the seed sources. Packer & Clay (2003) tested the separate effects of distance- and density-dependent mortality of *Prunus* seedlings by species-specific soil pathogens, and found that distance is a better predictor of mortality than density, probably because *Prunus* roots support those pathogens. Such relationship could also hold for pathogens that specialized on seeds, as proposed by Janzen (1970). Furthermore, seed predators may favour the vicinity of plants for reasons that are not related to the density of their food resources: granivores often tend to avoid foraging in open environments where the risk of predation (e.g. by raptors) is considerably higher than beneath plant canopies (e.g. Abramsky *et al.* 1998).

As with the seed dispersal kernel, we assume an exponential decline of the predators' abundance with distance, namely:

$$N = N(\rho) = \frac{2\beta}{\pi q^2} \exp\left(-\frac{2\rho}{q}\right) \quad \text{eqn 5}$$

where β represents the intensity parameter, i.e. the total predator number, and q is the distance parameter characterizing seed predation, i.e. the mean distance from the source at which seed predators are located.

MODEL SUMMARY

Substituting the components of equation 1 with their explicit formulations (equations 2 to 5) yields the model analysed in this paper:

$$\frac{dS(\rho, t)}{dt} = \frac{2\alpha}{\pi D^2} \exp\left(-\frac{2\rho}{D}\right) - \mu S(\rho, t) - \frac{2\beta}{\pi q^2} \exp\left(-\frac{2\rho}{q}\right) \frac{aS(\rho, t)}{1 + aT_h S(\rho, t)} \quad \text{eqn 6}$$

Each of the seven parameters of this model has distinct and clear ecological interpretation. However, to fully explore the associations between dispersal, predation and establishment, we need, in principle, to examine the effects of all possible combinations of all parameters on recruitment patterns. Because such a requirement would be overly demanding, we first focus on the distance parameters of both dispersal and predation. Then we focus on the plants' perspective and explore how the intensity and distance parameters of dispersal determine the recruitment patterns.

CALCULATING THE SURVIVORSHIP AND ESTABLISHMENT CURVES

For every fixed non-negative parameter setting, our model (equation 6) reaches a stable distribution of seeds at the equilibrium, i.e.:

$$\lim_{t \rightarrow \infty} S(\rho, t) = \bar{S}(\rho)$$

that is unique, in the sense that it is reached for any positive initial condition. Equilibrium is obtained by

setting the left-hand side of equation 6 to zero. The quantity $\bar{S}(\rho)$ describes the density of potential recruits, i.e. the establishment curve; it embodies all mortality occurring during the seed stage, but could still change during subsequent recruitment stages (Augspurger 1983; Schupp & Fuentes 1995; Schupp 1995; Nathan & Muller-Landau 2000).

The proportion of seeds escaping predation at any time t can be calculated as

$$P(\rho, t) = \frac{\mu S(\rho, t)}{\phi(\rho)}$$

which represents the dimensionless ratio of the density of surviving seeds in the presence of predators [$S(\rho, t)$] to that in their absence at the equilibrium [$\phi(\rho)/\mu$]. The dynamics of $P(\rho, t)$ would thus obey the equation

$$\frac{dP(\rho, t)}{dt} = \frac{\mu dS(\rho, t)}{\phi dt} = \mu(1 - P(\rho, t)) - N(\rho) \frac{a\mu P(\rho, t)}{\mu + aT_h P(\rho, t)\phi(\rho)} \quad \text{eqn 7}$$

The 'survivorship curve' $\bar{P}(\rho)$ is simply the proportion of seeds escaping predation at the end of the dispersal season, i.e. the equilibrium value of equation 7, which is equal to $\bar{P}(\rho) = \mu \bar{S}(\rho) / \phi(\rho)$. The survivorship curve $\bar{P}(\rho)$ and the establishment curve $\bar{S}(\rho)$ are then used to identify the predicted recruitment patterns, as explained below.

Results

THE MODEL GENERATES ALL OBSERVED RECRUITMENT PATTERNS

We can obtain all three basic recruitment patterns by varying only the average distances of dispersal (D , see Fig. 4) or predation (q , not shown); all other parameters, including the intensity parameters of dispersal (α) and predation (β), are kept constant. Note that while we do make assumptions about dispersal and predation, we do not make any assumptions about the patterns of survival and establishment: those patterns emerge mechanistically from the model. The recruitment patterns obtained by the model (Fig. 4) are qualitatively the same as those described conceptually (Fig. 2) and observed in the field. Thus, the negative distance-dependence of dispersal and predation is sufficient to generate all the commonly observed or hypothesized recruitment patterns. We also emphasize that although we do not force any coupling between the values of D and q , the dispersal of seeds and the spatial distribution of predators are to some extent coupled. By varying D and q over a wide range of values we simulate combinations of different seed dispersal processes that all give rise to declining seed densities but in different rates, and different predators that are all attracted to the seed sources but, again, in different rates.

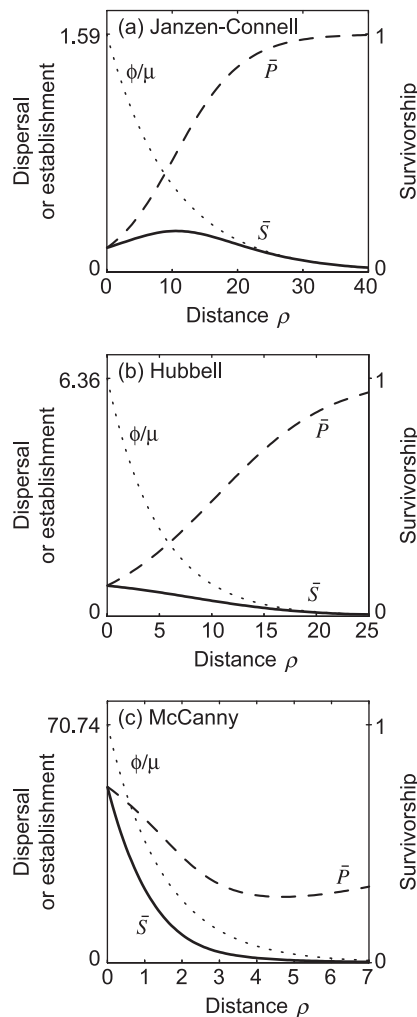


Fig. 4 The recruitment patterns obtained by the model: (a) Janzen-Connell, (b) Hubbell and (c) McCanny patterns. The plots are based on the following parameter setting: fecundity $\alpha = 100$, seed handling time $T_h = 0.1$, mortality not by predation $\mu = 0.1$, searching rate $a = 5$, predation intensity $\beta = 30$, mean distance of predators $q = 10$ and: (a) mean seed dispersal distance $D = 20$; (b) $D = 10$; (c) $D = 3$.

IDENTIFYING RECRUITMENT PATTERNS IN THE PARAMETER SPACE

To systematically explore how dispersal and predation affect the recruitment patterns predicted by our model (equation 6), one needs to distinguish between different recruitment patterns in some parameter space. As dispersal always decreases with distance from the source, different recruitment patterns can be identified according to the properties of the establishment and survivorship curves. If the establishment curve is unimodal and peaks at some distance from the source, as in J-C pattern (see Fig. 2a), an increase of the establishment curve close to the source, i.e.:

$$\left. \frac{d\bar{S}}{d\rho} \right|_{\rho=0} > 0$$

is the simplest condition for identifying this pattern. As shown in Appendix 1, this condition is equivalent to the following relationship:

$$\bar{P}(0) < 1 - \frac{q}{D} \quad \text{eqn 8}$$

The mathematical simplicity of this criterion (equation 8) is striking; it implies that the occurrence of the J-C pattern in our model depends exclusively on the proportion of seeds escaping predation at the source and the ratio between the predator and the seed dispersal average distances. As $\bar{P}(0)$ cannot be negative, criterion 8 requires that D is greater than q . It should be emphasized, however, that although the condition $D > q$ is necessary for the J-C pattern to occur in the model, it is not sufficient, because there may be other causes for the failure of the criterion described by equation 8.

If the establishment curve declines monotonically with distance, as in Hubbell or McCanny patterns, one must look at the survivorship curve $\bar{P}(\rho)$, obtained by setting the right hand-side of equation 7 to zero, to distinguish between these two patterns: $\bar{P}(\rho)$ increases in the former and decreases in the latter. As $\lim_{\rho \rightarrow \infty} N(\rho) = 0$, from equation 7 it is apparent that $\lim_{\rho \rightarrow \infty} \bar{P}(\rho) = 1$. Thus, it is important to choose an appropriate interval of distances $(0, \rho_{\text{far}})$ on the survivorship curve over which the trend of the survivorship curve should be estimated. To cover the distance over which most seeds are dispersed, it is useful to determine ρ_{far} as a high percentile (selected as the 95th percentile in our case) of the dispersal kernel. A simple quantity that qualitatively describes the trend of the survivorship curve is the difference $\Delta\bar{P} = \bar{P}(0) - \bar{P}(\rho_{\text{far}})$: we thus used the thresholds $\Delta\bar{P} > 0.05$ and $\Delta\bar{P} < -0.05$ to define the Hubbell and McCanny patterns, respectively. Alternative threshold values produced very similar results. The exact compensation and invariant survival patterns were identified as transitions between the three basic recruitment patterns.

RECRUITMENT PATTERNS AND THE DISTANCE PARAMETERS OF DISPERSAL AND PREDATION

Figure 5 illustrates how the recruitment patterns depend on the average distances of dispersal and predation. Each point in the parameter space corresponds to one recruitment pattern. The three basic recruitment patterns occupy most of this space, separated by the two transitional types.

According to our model, the J-C pattern, in which establishment is a unimodal function of distance, necessitates, as pointed out above, that the mean dispersal distance (D) is higher than the mean predation distance (q) (e.g. point A in Fig. 5). Accordingly, the J-C region in the (D, q) parameter space is a subset of the $D > q$ region, part of which is classified as Hubbell patterns. As envisioned by Janzen and Connell, the J-C pattern can occur if predators are strongly attracted to the proximity of the seed source and plants respond by dispersing seeds farther away to escape predation. The Hubbell pattern, in which establishment declines monotonically with distance despite an underlying trend of increasing escape, is located around the $D = q$ diagonal, i.e. it

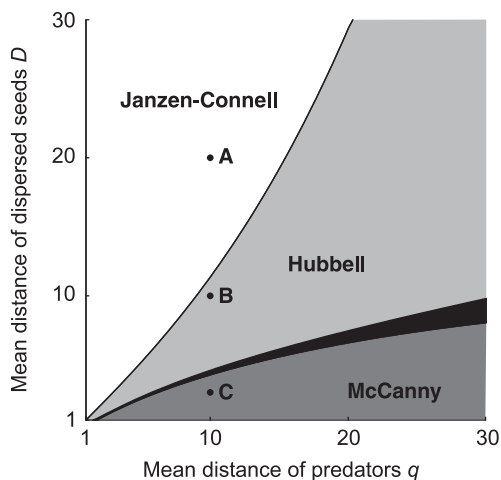


Fig. 5 The relationships between the distance parameters, of both dispersal (D) and predation (q), and the resulting recruitment patterns: Janzen-Connell (white region), Hubbell (light grey) and McCanny (dark grey) patterns. Transitions between the basic patterns (where present) are shown as black. The points marked with capital letters correspond to the recruitment patterns shown in Fig. 4. Unspecified parameter values are as in Fig. 4.

requires comparable magnitudes of dispersal and predation mean distances (e.g. point B in Fig. 5). The McCanny pattern, in which the strong decline in establishment results from monotonically declining escape, is located well below the $D = q$ diagonal, i.e. it requires dispersal distances considerably lower than mean predation distances (e.g. point C in Fig. 5).

As proposed in some earlier studies (e.g. Augspurger & Kitajima 1992; Burkey 1994), we find that predator satiation (Janzen 1971, 1976; Harper 1977) is the critical process underlying the McCanny pattern. If predators are strongly satiated near the source, the probability of seed survival can be higher there than farther away, thus leading to a McCanny pattern. For predator satiation to occur near the source, the number of seeds per predator should be larger than the number an average predator can eat. This can be obtained either by increasing seed density near the source through limited dispersal (low D), or by reducing predator density there (high q), or most effectively by doing both. Accordingly, Fig. 5 shows that the McCanny pattern is associated with a combination of relatively low D and high q .

RECRUITMENT PATTERNS AND SEED DISPERSAL

From a broader perspective, predator satiation could result also from plants dispersing more seeds overall, that is through increased fecundity (high α), which increases seed densities over all distances. Plant species exhibit substantial interspecific variation in the two basic components (D and α) of the dispersal kernel (Fig. 3). In particular, fecundity is highly variable, e.g. it ranges over four orders of magnitude among 14 tree species in Appalachian forests (Clark *et al.* 1998), and

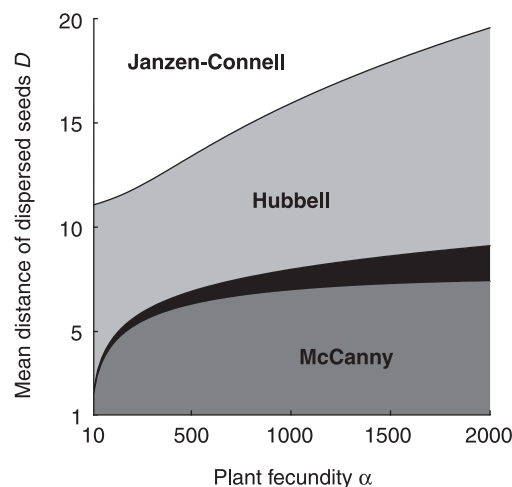


Fig. 6 The relationships between the parameters of seed dispersal (the mean distance of dispersed seeds (D) and plant fecundity (α)) and the resulting recruitment patterns. Unspecified parameter values are as in Fig. 4.

also varies considerably among individuals in the same population (Willson *et al.* 1990; Greenberg 2000) and among years (Silvertown 1980; Herrera *et al.* 1998). As we model the dispersal kernel to explicitly account for these two components, it is possible to explore their joint effects by employing the same procedure used in the previous section for q and D . We now partition the parameter space (α , D) into regions corresponding to different recruitment patterns (Fig. 6). Thus, this figure focuses on the determinants of recruitment patterns from the plants' perspective.

A combination of relatively high D and low α corresponds to (few) widely dispersed seeds, which are therefore able to escape predators attracted to the source. This embodies the mechanism behind the J-C model, and unsurprisingly produces that pattern (Fig. 6). While the Hubbell pattern requires a combination of relatively high D and high α , the McCanny pattern can be obtained only by limited dispersal (low D). As explained previously, limited dispersal may lead to seed densities near the source sufficient to satiate predators, thereby yielding escape probabilities that decrease with distance. Over the examined parameter space, invariant survival, which is transitional between the McCanny and Hubbell patterns, becomes more prevalent at higher α (Fig. 6): escape is roughly invariant with distance and thus the establishment curve is (almost) proportional to the dispersal curve. The interplay between high fecundity and predator satiation over space means that, as more seeds are dispersed (higher α), high seed densities satiate predators over a wider range of distances, resulting in nearly invariant survival.

ROBUSTNESS OF THE RESULTS

Our analyses so far have shown that the relationships between the parameters q , D and α , and the resulting recruitment patterns, are robust to changes in other

parameter values. We examined the consequences of changing not only the values for the parameters characterizing predation, but also the predator's functional response $\psi(S)$, replacing Holling's disc equation (equation 4) with another formulation of type II functional response (Spalinger & Hobbs 1992) and with classical forms of type I and type III functional responses (Hassell 1978). We observed only quantitative effects of these changes on how the parameter spaces (q, D) and (α, D) are partitioned among the recruitment patterns. We also performed the analysis presented above for a different version of the model, adjusted for a one-dimensional spatial context of a linear transect radiating from the source. The results were, again, comparable with those presented above. We note that the criterion for identifying J-C pattern (equation 8) is provable for this version as well.

Discussion

SEED PREDATION AS THE MECHANISM BEHIND THE DIFFERENT RECRUITMENT PATTERNS

Post-dispersal seed predation is often the major cause of mortality throughout a plant's life cycle, and one of the principal processes underlying plant recruitment patterns (see Introduction). Indeed, pre-dispersal seed loss, habitat heterogeneity, seedling competition, herbivory and other processes can also affect plant recruitment patterns (Schupp & Fuentes 1995; Nathan & Muller-Landau 2000). However, our work indicates that the attraction of seed predators to the vicinity of adult plants as a predictable zone to obtain food is sufficient, by itself, to generate the full range of observed and hypothesized recruitment patterns. It remains for future theoretical and empirical studies to elucidate the relative impact of different processes on recruitment patterns; we predict that seed predation will be ranked high among the most influential factors.

Our model provides the first mathematical reconstruction of Janzen's (1970) conceptual model, which supports his claims at three levels. First, it predicts survivorship and establishment curves that are remarkably similar to those in his graphical model (contrast Figs 4a and 1). Secondly, it confirms that the underlying forces proposed by Janzen (predators' attraction to the vicinity of adult plants and plants' farther dispersal to escape predation) would indeed result in the J-C pattern. Thirdly, we support the point made by Janzen that J-C effects are more likely to occur when seed predators are strongly host-specific (see also Hammond & Brown 1998). This is because specialized pests tend to concentrate their activity in areas of high densities of their plant host, i.e. beneath or in the immediate vicinity of fruiting plants, as compared with more generalized seed predators, who tend to prey on seeds also farther away (Howe *et al.* 1985; Terborgh *et al.* 1993; Pizo 1997). We emphasize that the same effects can be attributed to

differences in mobility among seed predators. Our distance parameter of predation (q) can therefore be related to the level of host-specificity, with lower values associated with more specialized predators; it may also be related to predator mobility, with lower values associated with less mobile predators. As we follow the continuum from a J-C to McCanny pattern (Fig. 2), the level of host-specificity decreases while the level of predator mobility increases. This closely matches the general argument made by Hammond & Brown (1998), by which seed/seedling attack by invertebrates, often highly host-specific and less mobile, is very likely to generate a J-C pattern, while vertebrates, often highly mobile and rarely host-specific, tend to generate other recruitment patterns.

We show that the J-C pattern does not restrictively require a 'minimal critical distance' (Hubbell 1980; Clark & Clark 1984), a range in the immediate vicinity of the adult in which the probability of survival is absolutely zero (see Fig. 1). However, unlike Janzen's assertion that distance- or density-dependent seed predation should predominantly result in a unimodal recruitment pattern, we show that it can also lead to all other patterns of recruitment observed in nature. (Indeed, to test whether or not this argument holds in reality, we need to examine which regions of the parameter space are possible in nature; see Models and reality below.) We also show that variation in fecundity does not only shift the peak of the establishment curve, as shown by Janzen (1970, his Figs 2 and 3), but can also generate other recruitment patterns, even with all other parameters remaining the same.

The Hubbell and McCanny patterns (the two other frequently observed and predicted recruitment patterns) share the same general trend of monotonically decreasing establishment with distance, but differ in the underlying survivorship curve, either increasing (Hubbell pattern) or decreasing (McCanny pattern). We support Hubbell's (1980) argument that the attraction of seed predators to adult plants can frequently lead to monotonically decreasing establishment. We find that the Hubbell pattern occurs if dispersal and predation have comparable magnitudes. This matching between predator and seed mean densities is equivalent to an ideal free distribution in which each predator has access to the same density of seeds. It corresponds to mobile predators that are not very host-specific, hence are not restricted to high plant host densities. Nevertheless, such optimal foraging by predators is the least favourable situation from the plant perspective and plants may respond in one of two ways (see Reducing the cost of predation: escape or satiate? below).

Our results also confirm McCanny's (1985) clarification that various qualitatively different recruitment patterns may be found in nature. However, his exact compensation type is practically impossible in its original description (Fig. 2b), and in our view simply represents the boundary between J-C and Hubbell patterns. However, we believe that invariant survival, the second

transitional recruitment pattern, is legitimate as not only does it occupy parameter space, but it has also been observed in nature and has a possible mechanistic explanation (predator satiation over all relevant space by increasing plant fecundity).

The McCanny pattern (Fig. 2e) has been observed frequently in nature and is predicted by our model. Predator satiation near the source provides a potential mechanism for this pattern, most effectively by a combination of limited dispersal and a low level of predators' attraction to adult plants. It corresponds to generalized and/or highly mobile seed predators, more likely vertebrates than invertebrates (Hammond & Brown 1998), who are attracted to parent plants, but frequently forage also farther away. Rapid satiation of generalized mammalian seed predators during mast events was reported for two tropical tree species, while specialized beetles were not satiated (Hart 1995). Because of the negative distance-dependent predation assumed in our model, the predator satiation mechanism yields an interesting and counterintuitive negative association between predator activity and predation rate: although the density of predators declines with distance from the source, the proportion of seeds eaten by seed predators increases.

To test the consistency of our model with the predator satiation explanation, we examine how the prevalence of the McCanny pattern in the (q, D) parameter space is affected by varying the seed-handling time T_h (Fig. 7). As T_h decreases, seeds are consumed faster once they have been found, and predators are less likely to be satiated. Accordingly, our model predicts a declining prevalence of the McCanny pattern as T_h decreases. This provides another indication that generalized seed predators (high T_h) are more likely to generate the McCanny pattern than specialized seed predators (low T_h). Studies of predator satiation give much attention to mast seeding events, when seed release is synchronized across individuals (Janzen 1976; Silvertown 1980; Crawley

1992; Kelly 1994; Herrera *et al.* 1998). However, satiation can also occur without synchronization (Augsburger & Kitajima 1992; Hammond & Brown 1998) and may be a common process affecting plant recruitment patterns. Our results therefore call for more emphasis on the spatial aspects of predator satiation, which have been relatively ignored in favour of the temporal aspects.

REDUCING THE COST OF PREDATION: ESCAPE OR SATIATE?

To assess the impact of seed predation on a plant's reproductive success, and the potential benefits or costs to plants with different dispersal strategies (different D 's), a measure for plant reproductive success is required. We followed Janzen's (1970, p. 502) emphasis that 'the area under this [establishment] curve represents the likelihood that the adult will reproduce at all, when summed over all seed crops in the life of the adult tree'. We thus examine how the total number of seeds escaping predation integrated over all distances (i.e. the area under the establishment curve) depends on D , for a fixed mean distance of predation (q). Indeed, Janzen's interpretation of the area under the establishment curve corresponds to the plant's reproductive success as he defined survival as the 'probability that seed or seedling will mature'. In our model, however, survival is only to the end of the seed stage; thus, the area under the establishment curve is the total number of surviving seeds, or the 'potential reproductive success'.

A recent theoretical investigation, using modelling approaches different from ours (Muller-Landau *et al.* 2003), showed that specialized pests can enforce strong selection for long-distance seed dispersal. Our study supports and extends these conclusions. The potential reproductive success is generally lowest at intermediate levels of dispersal; higher overall survival requires either low or high mean dispersal distances (Fig. 8).

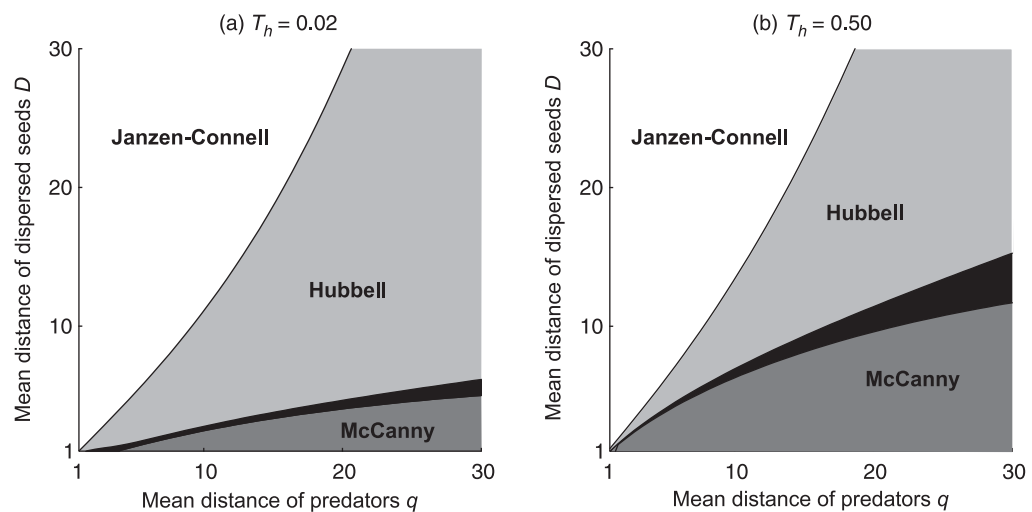


Fig. 7 The relationships between the distance parameters, of both dispersal and predation, and the resulting recruitment patterns for different values of the seed handling time (T_h): $T_h = 0.02$ (A) and $T_h = 0.50$ (B). The corresponding panel in Fig. 5 is obtained with $T_h = 0.10$. Unspecified parameter values are as in Fig. 4.

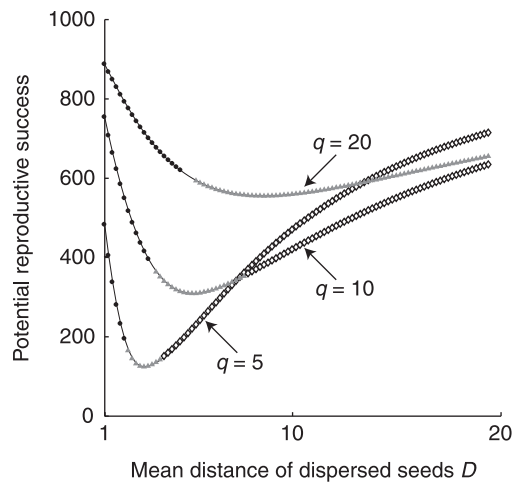


Fig. 8 Total potential reproductive success (i.e. the number of seeds surviving to the seedling stage) as a function of mean distance of dispersed seeds (D) for different values of the mean distance of predators (q), indicated by arrows. The marker styles represent different recruitment patterns: McCanny pattern (filled circles), Hubbell pattern (grey triangles) and J-C pattern (open diamonds). Other parameter values are as in Fig. 4.

This suggests two different strategies for a plant to decrease the cost of predation: dispersing farther to escape local predators in case of high average dispersal distances (J-C pattern) or dispersing more locally to satiate predators near the source in case of low average dispersal distances (McCanny pattern).

A recent study of dispersal and predation of pine seeds (Vander Wall 2002) suggests that in mast years, chipmunks and other animals that function as seed dispersers transport a larger number of seeds to longer distances than in non-mast years, whereas birds and other animals that function as seed predators are quickly satiated by high seed densities close to the trees. Our study suggests that plants may control the fate of their seeds even more directly, using both favourable strategies simultaneously by producing seeds with and without dispersal-aiding traits (i.e. dispersal dimorphism; Harper 1977; Venable 1985). To our knowledge, it has not yet been suggested that predation can lead to dimorphism in dispersal characteristics of seeds with identical benefits for predators. Inferences regarding evolutionary trends, however, should be made with caution, as survivorship patterns at later recruitment stages may alter these strategies. For example, seedling competition near the source or competition with the parent plant could result in increased mortality, thus diminishing the advantages of satiating seed predators. On the other hand, sites far from the adult plant may be less suitable for establishment than closer sites, thus diminishing the advantages of escaping far away.

MODELS AND REALITY

Simple models are valuable for identifying the effects and interactions of key factors in systems that are often

too complex to be understood by field studies alone, or by models that incorporate numerous factors concurrently (Noy-Meir 1975; Levin 1981; Gatto & Rinaldi 1987). The simple model we propose helps to understand how the interplay between seed dispersal by plants and seed predation by animals can explain the wide variety of frequently observed recruitment patterns. Previous studies have interpreted these qualitatively different recruitment patterns as products of different mechanisms (see Introduction). However, we have shown that all the observed and hypothesized patterns could result from simple variations of exactly the same rudimentary mechanism of predator attraction to the seed source that causes negative distance-dependent seed predation.

To bridge between our model and reality, we first need to explore which regions of the parameter space are possible in nature, and under which conditions. The minimal modelling approach facilitates this task because the focal parameters of the model are simple, distinct and quantifiable, and the results are testable against empirical data. In Table 1 we summarize the empirical data required to parameterize and test the models. For example, the criterion for J-C pattern (equation 8) can be tested by quantifying the average proportion of seeds escaping predation beneath the parent plant ($\bar{P}(0)$), and the mean distance of predators (q) and of dispersed seeds (D). $\bar{P}(0)$ and q can be estimated, respectively, by seed predation experiments, and by sampling predator densities at different distances from the seed source. We already know a great deal about how to obtain reliable field data on mean distance of (most) dispersed seeds D (Willson 1993), as well as plant fecundity α (Clark *et al.* 1998; Herrera *et al.* 1998) and the establishment curve \bar{S} (Hammond & Brown 1998). We emphasize that the major processes determining recruitment patterns operate at local scales; therefore, difficulties in estimating dispersal and establishment at large scales (Cain *et al.* 2000; Nathan 2001; Nathan *et al.* 2002, 2003) are not expected to impair the quantification of the above parameters.

DIRECTIONS FOR FUTURE RESEARCH

Simple models provide the impetus for further extensions. In our case, there are numerous possibilities: other sources of mortality (μ) could vary with distance (Hubbell 1980); distance-dependent seedling herbivores could act on \bar{S} as a 'second wave' of mortality agents to shape the realized recruitment pattern (Connell 1971; Schupp 1995; Nathan & Muller-Landau 2000); and seed predators could act also as dispersal agents (Janzen 1971; Harper 1977; Chambers & MacMahon 1994; Wenny 2000). On a more evolutionary perspective, the model could be extended to incorporate trade-offs between seed production, dispersal distances, seed predation rates and germination success, all closely related to seed size (Geritz 1998; Jakobsson & Eriksson 2000; Levin & Muller-Landau 2000).

Table 1 Summary of quantities, axes of variation and suggested empirical methods to estimate different parameters of the model

Parameters	Quantity	Varies with	Suggested empirical methods
D, α	Seed density (ϕ)	Distance	Field observations (e.g. seed traps)
μ	Seed mortality not associated with predation	Distance	Field experiments (e.g. seed trays protected from predation)
q, β	Predator density (N)	Distance	Field observations (censuses, soil samples, abundance estimators)
a, T_h	Seed intake rate (ψ)	Seed density	Field and laboratory experiments (manipulating seed densities)
\bar{P}	Seed probability to escape predation (\bar{P})	Distance mortality agents other than seed predators should	Field observations and experiments (seed trays; be controlled)
\dot{I}	Density of seeds available for germination (\dot{S})	Distance	Field observations and experiments (seed bank samples)

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Appendix 1: A criterion for identifying the Janzen-Connell pattern

Here we provide a mathematical justification for our central innovative finding that the J-C pattern depends on a simple criterion, merely the ratio between only two parameters. This criterion is not trivial, and thus needs to be formally and clearly justified.

Simplifying the notation of our model (equation 6), by omitting the dependence of ϕ , N and S on the distance ρ from the source, we obtain:

$$\frac{dS}{dt} = \phi - \mu S - N \frac{aS}{1 + aT_h S} \quad \text{eqn 9}$$

Differentiating the right-hand side of equation 9 with respect to ρ at the equilibrium (i.e. when $dS/dt = 0$), gives:

$$\frac{d\phi}{d\rho} - \mu \frac{d\bar{S}}{d\rho} = \frac{dN}{d\rho} \frac{a\bar{S}}{1 + aT_h \bar{S}} + N \frac{d}{d\rho} \left(\frac{a\bar{S}}{1 + aT_h \bar{S}} \right)$$

thus:

$$\frac{d\phi}{d\rho} - \mu \frac{d\bar{S}}{d\rho} = \frac{dN}{d\rho} \frac{a\bar{S}}{1 + aT_h \bar{S}} + \frac{aN}{(1 + aT_h \bar{S})^2} \frac{d\bar{S}}{d\rho} \quad \text{eqn 10}$$

As both seed dispersal ϕ and predator density N decline exponentially with distance (see equations 2 and 5), we can write:

$$\frac{d\phi}{d\rho} = -\frac{2}{D}\phi \quad \text{and} \quad \frac{dN}{d\rho} = -\frac{2}{q}N$$

At the equilibrium, from equation 9 we have:

$$\frac{aS}{1 + aT_h S} = \frac{\phi - \mu S}{N}$$

hence equation 10 can be rewritten as:

$$\frac{d\phi}{d\rho} - \mu \frac{d\bar{S}}{d\rho} = -\frac{2}{q}(\phi - \mu\bar{S}) + \frac{1}{N} \left(\frac{\phi - \mu\bar{S}}{\bar{S}} \right)^2 \frac{d\bar{S}}{d\rho} \quad \text{eqn 11}$$

Assuming that the two conditions $\bar{S}(0) > 0$ and $\lim_{\rho \rightarrow \infty} \bar{S}(\rho) = 0$ always hold in reality, a unimodal establishment curve can peak at some distance away from the source if and only if:

$$\left. \frac{d\bar{S}}{d\rho} \right|_{\rho=0} \equiv \bar{S}'(0) > 0$$

Setting $\rho = 0$ in equation 11 gives, after rearrangement:

$$\left[\mu + \frac{1}{N(0)} \left(\frac{\phi(0) - \mu\bar{S}(0)}{\bar{S}(0)} \right)^2 \right] \bar{S}'(0) = \frac{2}{q} (\phi(0) - \mu\bar{S}(0)) + \phi'(0) \quad \text{eqn 12}$$

where $\phi'(0) = \left. \frac{d\phi}{d\rho} \right|_{\rho=0}$. Because the expression in the square brackets on the left-hand side of equation 12 is always positive, condition $\bar{S}'(0) > 0$ is equivalent to requiring the right-hand side of equation 12 to be positive. This leads to the following inequality:

$$\bar{S}(0) < \frac{\phi(0)}{\mu} \left(1 - \frac{q}{D} \right) \quad \text{eqn 13}$$

Given that:

$$\bar{P}(0) = \frac{\mu\bar{S}(0)}{\phi(0)}$$

equation 13 can be rewritten to give criterion 8 (equation 8), that is:

$$\bar{P}(0) < 1 - \frac{q}{D} \quad \text{eqn 8}$$