Central-place seed foraging and vegetation patterns

Lorenzo Mari *,1, Marino Gatto, Renato Casagrandi

Dipartimento di Elettronica e Informazione, Politecnico di Milano, Via Ponzio 34/5, 20133 Milano, Italy

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**ABSTRACT**

We investigate how central-place seed foragers with a nest in the proximity of one or more seed sources determine the formation of different vegetation patterns. In particular, we discuss the ecological conditions that lead to the formation of hump-shaped (Janzen–Connell) patterns in a two-dimensional landscape. Our analysis shows that central-place predation can generate Janzen–Connell patterns even if predators’ movement strategies are exclusively based on resource abundance, both in the single-plant/single-nest case and in a forest with several seed sources. We also show that social foraging may either promote or work against the formation of Janzen–Connell patterns, depending upon the way foragers take advantage of social interactions.

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1. Introduction

Although seed dispersal generally declines with distance from the seed source, spatial patterns of seedling establishment can have several distinguishing shapes, ranging from monotonically decreasing to hump-shaped [McCanny, 1985]. The mismatch between the patterns of seed dispersal and seedling establishment has been commonly ascribed to post-dispersal seed predation, along a research line opened by the ground-breaking works of Janzen (1970) and Connell (1971). In fact, if specialized seed predators are attracted to the proximity of the seed source, then seed survival may increase with distance from the parent plant; this, combined with the decreasing densities of dispersed seeds, can actually lead to the formation of hump-shaped establishment patterns, generally referred to as ‘Janzen–Connell’ (J–C) patterns.

Post-dispersal seed predation is a key mechanism for pattern formation in plant ecosystems. Janzen (1970) and Connell (1971) suggested that the J–C pattern should favor spacing among conspecifics and the widespread formation of regular patterns of plant distribution over a landscape. However, the J–C pattern is just one of the possible outcomes of post-dispersal seed predation (McCanny, 1985). Field surveys have indeed shown that conspecific trees are often clumped, most notably in tropical forests (Condit et al., 2000). However, spatial clumping seems to be weaker for the largest and most common species (Condit et al., 2000; Muller-Landau and Adler, 2007). Therefore, the picture is far from being clear and the role of seed predation in the formation of vegetation patterns would deserve in-depth investigations. Quite surprisingly though, very few works in the literature have been devoted to a formal analysis of this subject in a spatially explicit setting. Nathan and Casagrandi (2004) proposed a simple mechanistic model aimed at showing that post-dispersal seed predation is indeed sufficient to explain the variability of seed establishment patterns found in nature. In particular, they focused on the effects of distance-dependent predation. In their model, the foragers’ spatial displacement is time-invariant and exponentially decreasing with distance from the seed source. Mari et al. (2008) have extended the approach introducing a partial differential equation (PDE) model that explicitly incorporates predators’ movement strategies. This represents a crucial modeling task, since both empirical and theoretical evidence show that seed predators can profoundly affect the spatial patterns of plants at the ecosystem scale (Armstrong and Roughgarden, 2005).

In the framework proposed by Mari et al. (2008), seed predators are allowed to move towards nearby locations according to both undirected (diffusive) and directed (tactic) movements. In particular, taxis depends on the foragers’ ability to evaluate the environmental quality of the surrounding landscape. From a technical standpoint, navigated motion capacities (sensu Nathan et al., 2008) are described in the model by Mari et al. (2008) via a deterministic adimensional functional \( f(x, y, t) \), named ‘habitat suitability’ after Fretwell and Lucas (1969), that indicates the attractiveness for seed predators of a given location \((x, y)\) at time \(t\). Via \( f(x, y, t) \) it is possible to analyze how movement strategies based on different cues (namely, seed density, distance from the seed source and density of conspecific predators) may generate different seed establishment patterns. In this way the authors formally showed that purely density-dependent seed predation cannot originate J–C recruitment patterns, while attraction to the seed source or to conspecifics can produce hump-shaped patterns.
The nature and number of the characteristics that make a location more or less suitable to a seed forager has been the subject of much discussion. Resource abundance is obviously considered as a crucial driver of foragers’ movement, because locations with high resource densities are in general preferred by predators (e.g., Fretwell and Lucas, 1969). Nevertheless, predators of seeds may also use other cues to navigate the surrounding environment. For example, distance from the seed source has been advocated as an important signal for seed foragers (distance-dependent predation; Janzen, 1970). On the other hand, seed predation is often exerted by animals whose focal place of activity is a nest that can be located at a certain distance from the seed source, a phenomenon commonly referred to as ‘central-place foraging’ (Ortians and Pearson, 1979; Stephens and Krebs, 1986; Olsson et al., 2008), here acrony whole for brevity as CPF. Examples of central-place foragers range from birds (e.g., Kacelnik, 1984; Johnst et al., 2001) to granivorous mammals (both small, e.g., Bowers and Ellis 1993, and large, Lewison and Carter 2004) and insects, most notably ants (Hölldobler and Wilson, 1990). Ants are in fact particularly important as post-dispersal seed predators in desert ecosystems and in the southern hemisphere, while they tend to act as seed dispersers in more humid environments (see Hulme and Kollmann, 2004). In the case of CPF, distance from the nest (rather than from the seed source[s]) can represent the most important component of habitat suitability for seed predators. In fact, proximity to the nest is not only useful for providing foragers with a refuge in case of carnivore attacks, but it also implies lower energetic costs during searching activities. In general, being far from the nest is ceteris paribus disadvantageous, as confirmed by studies on habitat selection by central-place foragers (e.g., Rosenberg and McKelvey, 1999; Naef-Daenzer, 2000; Nemeth et al., 2005).

The abundance of nestmates in a given location can also represent an important hint used by social predators to orient their movement. Simple attraction among conspecifics is generally referred to as ‘congregation’ (Turchin, 1998). In the context of seed predation, the local abundance of foraging nestmates that manage to find food items can be used by predators to gather information about the distribution of the resource they feed on. Depending upon species, individuals can be either attracted to or repelled by foraging conspecifics. These two cases are referred to in the literature as ‘local enhancement’ (Turner, 1994b; Pöysä, 1992; Buckley, 1997; Grünbaum and Veit, 2003; Slaa et al., 2003; Silverman et al., 2004) and ‘local inhibition’ (Goulson et al., 1998; Slaa et al., 2003), respectively. In particular, local enhancement can be used by foragers to locate patches with high resource density, whereas local inhibition can be used to avoid overexploited patches. Social interactions among foragers do not always require the reception of direct stimuli. For instance, the foragers of many species of harvesting ants produce pheromones when they find food items and carry them back to the nest. Individuals of these species can thus establish foraging trails that help nestmates navigate the environment and efficiently locate resources (Hölldobler and Wilson, 1990). Other cues could in principle be used by seed predators to orient their movement (like the abundance of carnivores or competitors), but in this study we limit our attention to the interaction between seeds and their consumers.

The goal of the present work is to explore how CPF influences the spatiotemporal characteristics of seedling establishment and, in turn, of vegetation patterns. The particular focus of the present work is to discuss which ecological conditions can favor the formation of J–C patterns under CPF. We specifically consider predators that use seed density, distance from the nest and social interactions to navigate the surrounding landscape. Here, we do not account for the foragers’ response to distance from the seed source[s]. The reason of this choice is twofold. On the one hand, as already remarked above, the most important distance-dependent component of foragers’ movement strategies under CPF is attraction to the nest. On the other hand, it has already been shown elsewhere (Nathan and Casagrandi, 2004; Mari et al., 2008) that attraction to the seed source alone can generate J–C patterns. We use a PDE model based on Mari et al.’s (2008) framework, with some important novelties. First, the model presented here is set in an explicit two-dimensional (2D) landscape, which makes the analysis of seed predation more realistic (Nathan and Casagrandi, 2004), already considered a 2D model, but they reduced it to 1D due to isotropy). Second, we analyze cases in which multiple seed sources are displaced over the landscape, so that seed shadows can overlap. Third, we study several types of social interactions among seed predators and analyze the influence of social foraging on the formation of vegetation patterns. In particular, we generalize the model by Mari et al. (2008) to embrace situations in which purely density-dependent predators have a specific center of activity that does not coincide with the seed source, but with their nest. We specifically address the case in which seed foragers share the same nest, as in most harvester ant species. Using the model, we study how predators’ movement strategies, environmental factors and behavioral characteristics interact to determine the emergence of different seed establishment patterns.

2. The model

The problem of post-dispersal seed predation exerted by central-place foragers can be more realistically analyzed in a 2D spatial setting than in the simple 1D scenario used in Mari et al. (2008). Also, to make the model as general as possible, we consider here the possibility that there exist multiple seed sources producing overlapping seed shadows.

2.1. Model equations

The 2D version of the PDE model proposed in Mari et al. (2008) reads as

\[
\frac{\partial S(x, y, t)}{\partial t} = \Phi(x, y) - \mu S(x, y, t) - \psi(S(x, y, t)) N(x, y, t)
\]

and

\[
\frac{\partial N(x, y, t)}{\partial t} = -cV \cdot \nabla f(y, x, t) \frac{N(x, y, t)}{1 + \delta N(x, y, t)} + \delta V^2 N(x, y, t),
\]

where the symbol \( \nabla \) stands for \( \partial_x + \partial_y \). Eqs. (1)–(2) describe the dynamics of the density per unit area of seeds \( S(x, y) \) and of predators \( N(x, y, t) \) at location \( (x, y) \) and time \( t \).

The first equation is Nathan and Casagrandi’s model (2004), which describes the temporal dynamics of seed density on the ground as a balance between one gain term, namely the total seed input rate due to dispersal \( \Phi(x, y) \), and two loss terms due to natural mortality and predation exerted by seed foragers. The parameter \( \mu \) represents the natural mortality rate, which is assumed to be constant. Mortality due to predation is the product between the consumer density \( N(x, y, t) \) and the predators’ functional response \( \psi(S) \). We remark that all potential causes of seed removal other than predation or natural mortality (like for example secondary dispersal or autotoxicity) are not accounted for in the present approach. As a consequence, the density of seeds at the end of the dispersal season can serve as an indicator of the density of potential recruits. Each of the \( k = 1, 2, \ldots, m \) plants composing the forest under study contributes to the total seed input \( \Phi(x, y) \) . We assume that the seed dispersal kernel \( \phi(x, y) \) of the generic \( k \)-th plant in the forest is time-invariant during the dispersal season and exponentially decreasing with distance from the parent plant. Other choices would have been possible.
(e.g., Nathan and Muller-Landau, 2000), in particular to account for fat-tailed seed shadows (see Section 4). The local seed input $\Phi (x, y)$ can thus be expressed as

$$
\Phi (x, y) = \sum_{k=1}^{m} \phi_k (x, y) = \sum_{k=1}^{m} \frac{2a_k}{\pi D_k} \exp \left( - \frac{2(x-x_k)^2 + (y-y_k)^2}{D_k} \right),
$$

where $a_k$ and $D_k$ are respectively the total seed output of the $k$-th plant and the mean distance traveled by the seeds dispersing from it, whereas the pair $(x_k, y_k)$ represents the spatial coordinates of the $k$-th seed source. The functional response $\psi$ is assumed to be of Holling type II (Holling, 1959), i.e.,

$$
\psi (S(x, y), t) = \frac{a S(x, y, t)}{1 + aT_b S(x, y, t)},
$$

where $a$ and $T_b$ are the predator’s searching rate and handling time, respectively. These two quantities are assumed here to be space-independent. Such a choice could in principle represent an oversimplification in some CPF problems, because the searching rate might be influenced by distance from the nest (Olson et al., 2008). However, Holling type II functional responses have been successfully parameterized for harvester ants with data based on field experiments (Avgar, 2006). The effects of using alternative functional responses to describe seed predation are discussed in Section 4.

As in Mari et al. (2008), Eq. (2) describes the spatiotemporal dynamics of $N(x, y, t)$ as resulting from movement only. In fact, the demography of foragers is disregarded in the model and the total abundance of predators is kept constant over time, i.e.,

$$
\beta = \int_0^\infty dy \int_0^\infty N(x, y, t) dx.
$$

This hypothesis is acceptable provided that the seed dispersal season is shorter than the predators’ average lifetime, as it typically is. Eq. (2) separately accounts for undirected (diffusive) and directed (tactic) movements. The parameters $\delta$ and $\epsilon$ represent the pure diffusion and the taxis coefficients (sensu Okubo and Levin, 2001). Diffusion coefficients can be estimated, for example, by means of inverse modeling techniques or individual tracking methods (Turchin, 1998; Okubo and Levin, 2001). The value of $\delta$ used in numerical experiments is derived from Tuda and Shima (2002), where the estimation of the diffusion coefficient for a population of insect predators is described. On the contrary, measuring the directed component of movement still represents a challenging problem (Holyoak et al., 2008). Therefore, no reliable estimates for $\epsilon$ are available and we let it vary widely around the value of $\delta$ (notice that $\epsilon$ and $\delta$ can be measured in the same units, since habitat suitability $f$ is assumed to be adimensional).

Directed movement depends on the strategy adopted by seed predators and thus represents an explicit link between the foragers’ behavior and the resulting seed recruitment patterns. In particular, movement is oriented in the model according to how suitable the surrounding environment is for the foraging activity of the seed predator. Suitability is generally described by a function $f(x, y, t)$ that accounts for those characteristics of the environment that a predator can use to orient its movement (see Section 1). Among the many environmental cues possibly used by a central-place forager, the most important are seed and conspecific densities, together with the distance from the nest. Therefore, in the case of CPF we assume that $f(x, y, t)$ can be written as

$$
f(x, y, t) = F (h(x, y), S(x, y, t), N(x, y, t)),
$$

where $h(x, y)$ is the distance between the current predator spatial location $(x,y)$ and the nest position $(x_n, y_n)$. We assume a 2D Euclidean topology for the landscape corresponding to a flat territory, that is

$$
h(x, y) = \sqrt{(x-x_n)^2 + (y-y_n)^2}.
$$

The exact dependence of $F$ on $h$ details how CPF is accounted for. In particular, in the present work we assume a linear relationship between $F$ and $h$. Although such a simple choice is of course plausible, we remark that it is not the unique possibility. For example, antipredator behavior of seed foragers might induce constraints on the maximum distance from nest traveled by seed predators during their searching activities (Lima, 1990).

Some general biological principles that determine the suitability of a location translate into the following properties of $f$:

(i) the function $F$ is non-increasing with distance from the nest ($\partial F/\partial h \leq 0$);

(ii) $F$ is non-decreasing with seed abundance ($\partial F/\partial S \geq 0$).

Depending on the social behavior of the species under study, the habitat suitability function can also be either increasing with conspecific density ($\partial F/\partial N > 0$, congregation) or decreasing ($\partial F/\partial N < 0$, repulsion). More complex social interactions are of course possible and can be accounted for by the model. Further hypotheses describing predators’ social habits will be introduced later in the paper.

### 2.2. Plant recruitment patterns in 2D landscapes

Being set in a 2D spatial landscape, model (1)–(2) is not completely amenable to formal analytical investigations. Therefore, it is studied via numerical analysis. From a technical viewpoint, we integrate the PDE system with a standard explicit Euler method in time and a finite difference numerical scheme on a structured square mesh in space (Strikwerda, 1989). The time step and the grid size are suitably chosen in order to ensure both the stability and the computational efficiency of the numerical scheme. The number of time steps performed is large enough so as to let the resulting plant recruitment patterns and predator spatial distributions reach a stationary condition. Steady seed and predator distributions are denoted by $\tilde{S}(x, y)$ and $\tilde{N}(x, y)$, respectively.

As stated above, we are particularly interested in determining the ecological conditions that lead to hump-shaped J–C patterns. Establishment patterns in 2D settings with a single seed source can be studied by means of the radial distribution of seed densities $\tilde{S}(\rho)$ as a function of distance $\rho$ from it (Pearl, 1985; Nathan and Muller-Landau, 2000), which also represents the quantity usually estimated in the field (e.g., Hubbell, 1979; McCann and Cavers, 1987; Howe, 1993; Queenborough et al., 2007; Avgar et al., 2008). This function can be evaluated as

$$
\tilde{S}(\rho) = \frac{1}{2\pi} \int_0^{2\pi} \tilde{S}(\rho, \theta) d\theta,
$$

where $\tilde{S}(\rho, \theta)$ is the density of seeds at the equilibrium that are at distance $\rho$ from the seed source along the angular direction $\theta$. In plain words, $\tilde{S}(\rho)$ represents the average seed density per unit area [seeds m$^{-2}$] at a distance $\rho$ from the seed source. Note that $\tilde{S}(\rho, \theta)$ can be easily estimated from the stationary seed establishment $\tilde{S}(x, y)$ by switching to polar coordinates.

An important remark is that the radial distribution of seed densities per unit area $\tilde{S}(\rho)$ must not be confused with the radial distribution of seed numbers per unit length

$$
\tilde{S}_L(\rho) = \int_0^{2\pi} \rho \tilde{S}(\rho, \theta) d\theta,
$$

which represents the total number of seeds contained in a 1-meter annulus at distance $\rho$ from the source [seeds m$^{-1}$]. By dealing
with \( \tilde{S}(\rho) \), in fact, we ensure that monotonically decreasing 2D seed establishment patterns give rise to monotonically decreasing radial distributions. On the contrary, had we used seed density per unit length, we would have found that even monotonically declining 2D establishment patterns can produce a hump in the \( \tilde{S}(\rho) \) distribution. This side effect is due to the fact that the increase of the areas of the annuli surrounding the seed source at increasing distances from it is larger than the decline of seed dispersal (see the relevant discussion in Mari et al. 2008).

In the studies by Nathan and Casagrandi (2004) and Mari et al. (2008) a pattern is classified as J–C if the radial distribution of seed densities per unit area \( \tilde{S}(\rho) \), which is radially symmetric around the plant, exhibits a local minimum at the seed source. In fact, this condition implies that seed density is maximum at some distance away from the seed source, since seed density must vanish for very large distances from the seed source. Instead, when studying predators with a nest placed away from the center of the seed shadow, this local test is not sufficient to identify hump-shaped patterns, because the seed distribution can be radially asymmetric. In other words, there may be a hump in the radial seed distribution even if the seed source is not a local minimum of seed density. This complication arises also in the case of multiple seed sources.

Therefore, in the present study we identify a pattern as J–C if and only if its radial distribution of seed densities \( S(\rho) \) displays a global maximum whose location does not coincide with that of the seed source. This translates into the following condition

\[
\max_{0 < \rho < \infty} \tilde{S}(\rho) > 1. \tag{4}
\]

To evaluate condition (4) numerically, we introduce a threshold \( \gamma \). Specifically, a pattern is classified as J–C if \( r > 1 + \gamma \), whereas decreasing patterns are characterized by \( r < 1 - \gamma \). Patterns with \( r \approx 1 \) (numerically identified by \( |r - 1| < \gamma \)) correspond to the so-called ‘Exact Compensation’ pattern proposed by McCanny (1985). These patterns represent the most critical cases in the field, because small deviations from the value \( r \approx 1 \) could be statistically insignificant due to experimental noise. Condition (4) obviously reduces to that used in previous studies by Nathan and Casagrandi (2004) and Mari et al. (2008) if the foragers’ focal place of activity corresponds to the seed source.

Evaluating the emergence of J–C patterns via criterion (4) is simple also in cases in which several seed shadows overlap in the landscape. In the empirical literature, spatial patterns of seed establishment originated by multiple overlapping seed sources are typically discussed on the basis of the radial distribution of seed densities evaluated as a function of the distance \( \rho^* \) from the nearest conspecific adult (e.g., Hubbell et al., 1990; Wills et al., 1997). Technically, \( \rho^* \) can be easily evaluated by partitioning the spatial domain in regions lying within fixed distances from the nearest plant and computing the density of seeds therein (see Fig. 2 in Condit et al. 1992 and Fig. 1 in Nathan et al. 2000 for two typical examples of experimental designs). In this way, the test for the identification of J–C patterns previously described can be easily applied also to the case of overlapping seed shadows by simply replacing \( \rho \) with \( \rho^* \).

### 3. Results

Given the definitions stated above, model (1)–(2) allows us to numerically evaluate under which conditions hump-shaped J–C patterns can emerge. We analyze the cases of density dependent CPF (i) in a landscape with a single plant, (ii) in a forest with multiple seed sources, and (iii) when exerted by social foragers. Specifically, we study the role of both behavioral and landscape factors in determining the formation of different vegetation patterns.

#### 3.1. Central-place foraging and density-dependent seed predation with one single seed source

To explore the interplay between CPF and density-dependent seed predation, we use the following habitat suitability function

\[
f(x, y, t) = bS(x, y, t) - eh(x, y), \tag{5}
\]

in which \( b \) and \( e \) are two positive parameters accounting for the predators’ sensitivity to seed abundance and distance from the nest, respectively. Assuming a linear decrease of \( f \) with respect to \( h \) corresponds to imposing a negative exponential spatial distribution of predators around the nest in absence of seeds (Mari et al., 2008). Different and more complicated assumptions for the dependence of habitat suitability on distance from the nest are of course possible. For instance, some authors (e.g., Naef-Daenzer, 2000) provide evidence for a nonlinear decrease of habitat suitability with respect to the distance from the predators’ central place of activity. Our simple choice is however supported by field data (Andersson, 1981) and is frequently used in the literature (e.g., Nathan and Casagrandi, 2004; Adler and Muller-Landau, 2005).

Because of the landscape anisotropy introduced by the predators’ nest, density-dependent seed predation under CPF Eq. (5) can produce establishment patterns that were not obtainable with the model of Mari et al. (2008), in which the nest was not present. Fig. 1 contrasts a case of low \( e \) with one of high \( h \) and shows that a hump can appear in the seed establishment pattern \( \tilde{S}(x, y) \) close to the nest (panels a and d) because of the clumping of the predators’ distribution \( N(x, y) \) around the nest itself (panels b and e). As a result, a local peak of seed density can be recorded at a certain distance from the parent tree on the side opposite to the nest. Depending on parameter values, though, the radial distribution of seed density \( \tilde{S}(\rho) \) evaluated from the establishment patterns of Fig. 1 can display either a well-defined peak (panel c, low \( e \)) or a monotonically decreasing shape (panel f, high \( e \)). This finding is of particular interest, because it shows that density-dependent seed predation under CPF can produce hump-shaped seed establishment patterns, while purely density-dependent predation exerted by foragers with no nest cannot give rise to J–C patterns, as proved in Mari et al. (2008).

Fig. 1 also reveals that the existence of a local minimum in the seed establishment surface close to the nest does not necessarily imply the formation of a J–C pattern. In particular, a hump-shaped radial distribution of seed densities emerges if seed predators are not very sensitive to distance from the nest, thus exploring long distances from it in search for food (top panels of Fig. 1). On the contrary, if the attraction to the nest is high (bottom panels), then \( \tilde{S}(\rho) \) is monotonically decreasing.

The two parameters characterizing the core of predators’ movement strategies in model (1)–(2) are the sensitivity to seed density \( b \) and that to distance from the nest \( e \). Fig. 1 has already shown that different values of \( e \) are per se sufficient to produce a switch between J–C and monotonically decreasing patterns. Different values of \( b \) can originate qualitatively different patterns as well. To systematize the discussion, we have performed an analysis of the outcomes of model (1)–(2) with habitat suitability (5) and one single seed source, in the parameter space \( (b, e) \). Fig. 2a reveals that hump-shaped patterns can emerge in cases in which the predators’ sensitivity to the distance from the nest actually assumes intermediate values (corresponding to the light gray region). If predators are too attracted to the nest (high \( e^* \)), their equilibrial distribution is too clumped to generate a J–C pattern (remember Fig. 1e). On the other hand, predators that explore too large areas far from their central place of activity (low \( e^* \)) cannot produce hump-shaped patterns either. In fact, in the limit of \( e \to 0 \) the attraction towards the focal place vanishes and seed consumers become purely density-dependent foragers.

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Fig. 1. Simulations of model (1)–(2) with the habitat suitability function (5) and one single seed source. Panels a and d [b and e] show the stationary distribution of seeds $\tilde{S}(x, y)$ [predators $\tilde{N}(x, y)$] for two different values of the sensitivity to distance from the nest ($e = 0.5$, top panels; $e = 2$, bottom panels). Note that different axis limits are used in left and middle panels. The seed source is located in $(0, 0)$, where the dashed lines cross, while the position of the predators' nest $(x_n = 10/\sqrt{2}, y_n = -10/\sqrt{2})$ is marked by a white star (panels b and e only). The seed source and the nest are assumed to be points in space. Panels c and f show the stationary radial distribution of seed densities $\tilde{S}(\rho)$ as a function of distance $\rho$ from the seed source. Computations have been performed on a $60 \times 60$ square grid with zero-flux boundary conditions and a time step of 0.01. The model has been run for $10^4$ time steps in order to ensure convergence toward the stationary solution. Other parameter values are $m = 1$, $d_n = 10$, $\alpha = 1000$, $D = 20$, $\mu = 0.1$, $a = 1.44$, $T_0 = 0.0035$, $\beta = 400$, $\delta = e = 2.4$, $b = 1$.

Fig. 2. Patterns generated by model (1)–(2) with the habitat suitability function (5) and one single seed source for different choices of parameter settings. White, light gray and dark gray regions mark parameter combinations leading to monotonically decreasing, J-C or Exact Compensation patterns, respectively. The value of $\gamma$, as defined in the text, has been set to 0.05, while $\beta = 1600$. For each parameter setting, the model has been integrated on a $30 \times 30$ square grid. Unspecified parameter values and other simulation details as in top panels of Fig. 1.

and cannot produce hump-shaped patterns (see above). Notice also that if predators are very sensitive to seed abundance (high $b$’s), the relative contribution of distance from the nest to habitat suitability is low. In the limit of $b/e \to \infty$, predators “lose memory” of the position of their focal activity place, thus de facto turning again into purely density-responsive seed predators (that cannot
cause J–C patterns to emerge. As a result, they produce the Exact Compensation pattern (McCanny, 1985), characterized by almost constant recruitment over space (i.e., \( r \approx 1 \)). This result is clearly visible in Fig. 2a for low values of \( e \) (dark gray region).

The parameters of the habitat suitability function \( f \) are not the unique drivers of predators’ movement, since foraging behavior is influenced by taxis and diffusion coefficients as well. Fig. 2b shows that different values of \( \delta \) and \( \epsilon \) can actually lead to different establishment patterns. Specifically, increasing values of the taxis coefficient have a positive effect on the formation of J–C patterns, while an increase of the diffusion term is detrimental for the emergence of hump-shaped patterns. The characteristics of the seed source and the nest are also important in shaping establishment patterns. For instance, local densities of seeds and predators are obviously influenced by the plant fecundity \( \alpha \) and the total number of predators \( \beta \). Fig. 2c shows that J–C patterns are found if predation intensity \( \beta \) is sufficiently high. Also, for large \( \alpha \)’s monotonically decreasing patterns do not emerge for the parameter settings we explored. The shape of recruitment patterns is crucially determined also by the distance parameters of the model. In fact, Fig. 2d shows that J–C patterns are possible only if the plant-to-nest distance \( d_n = \sqrt{(x_n - x_i)^2 + (y_n - y_i)^2} \) is smaller than the mean distance \( D \) traveled by the dispersed seeds, at least for the parameter combinations considered here. This finding mirrors the condition proposed by Nathan and Casagrandi (2004) and is similar to the results of other works in spatial dynamics (Bolker and Pacala, 1997; Law et al., 2003), where it has been shown that spacing among conspecific trees (the fingerprint of the J–C pattern, see Section 1) is possible only if the mean seed dispersal distance is larger than the mean distance at which competition among parent plants occurs. Although mediated by different processes (seed predation here and in the paper by Nathan and Casagrandi, intraspecific competition in the works by Bolker and Pacala and Law et al.), the spacing mechanism is generated by the mismatch between the scales of seed dispersal and density dependence.

3.2. Density-dependent central-place foraging with multiple seed sources

The analysis just performed can be extended to investigate seed establishment patterns generated by central-place foragers in a forest with multiple seed sources. Different spatial arrangements of \( m \) trees can be considered. Fig. 3 shows three simulations of model (1)–(2) with the habitat suitability function (5) in an idealized forest composed by several individual trees (\( m = 10 \) in top and middle panels, while in bottom panels \( m = 14 \)) that are located around the predators’ nest according to a regular (top panels), random (middle panels), or clumped distribution (bottom panels). In this last case, forest geometry has been extracted from Fig. 11 in Nathan et al. (2002). The average distance of seed sources from the predators’ nest in both the random and the clumped scenarios has been set equal to the plant-to-nest distance in the first, regular case. Also, the values of the model parameters have been set in such a way that they would produce a J–C pattern in the single-tree case. As expected, the spatial configuration of seed sources influences the spatial displacement of seeds and foragers (panels a and b, d and e, and g and h). However, for the parameter setting used, each of the three forest geometries produces in any

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**Fig. 3.** Simulations of model (1)–(2) with the habitat suitability function (5) in the case of multiple seed sources (\( m = 10 \)). Panels a, d and g [b, e and h] show the stationary distributions of seeds \( S(x, y) \) foragers \( N(x, y) \). Note that different axis limits are used in left and middle panels. Plant locations are identified by white stars. The predator’s nest is located in (0, 0), where the dashed lines cross. Panels c and f display the radial distribution of seed densities \( S(\rho^*) \) as a function of distance \( \rho^* \) from the nearest plant. To numerically evaluate \( S(\rho^*) \), the spatial domain has been partitioned in regions lying within fixed distances from the nearest plant. In top panels trees are located on the vertexes of a regular polygon (\( d_n = 10 \)). In middle panels seed sources are displaced according to a bivariate normal distribution (the mean plant-to-nest distance is equal to 10). In bottom panels plant locations are adapted from Nathan et al. (2002) so that the mean plant-to-nest distance is equal to 10. Parameter values: \( \alpha_i = 1000 \), \( D_i = 20 \) (\( i = 1 \ldots m \)), \( b = 3 \). Other parameters and simulation details as in the top panels of Fig. 1.
Fig. 4. Patterns generated by model (1)–(2) with the habitat suitability function (5) and multiple overlapping seed sources for different choices of parameter settings. Panels a-b, c-d and e-f refer to the regular, random or clumped distributions of seed sources used in Fig. 3, respectively. White, light gray and dark gray regions mark parameter combinations leading to monotonically decreasing, J–C or Exact Compensation patterns. Dashed curves represent the boundary of the J–C region in the single-plant scenario (Fig. 2). Parameter values and simulation details as in Fig. 2.

Establishment patterns and steady predator distributions are of course influenced by behavioral and environmental parameters also in a landscape with multiple overlapping seed shadows. Therefore, we have performed the analysis of the model outcomes with respect to some relevant parameters. Specifically, we have focused on the habitat suitability parameters $b$ and $e$, on the abundance $\beta$ of predators and on the fecundity $\alpha$ of plants, for the three plant displacements just introduced. For the sake of simplicity, we assume that all seed sources have the same biological characteristics, i.e., $\alpha_k = \alpha$ and $D_k = D$ $\forall k$. Panels a, c and e of Fig. 4 show that the presence of multiple seed sources does not qualitatively modify the shape of the J–C region in the parameter space $(b, e)$ with respect to the outcomes obtained with a single seed source (dashed line). Therefore, J–C patterns are still expected for intermediate values of the sensitivity $e$ to distance from nest. From a quantitative point of view, though, the J–C region turns out to be remarkably larger in a landscape with multiple seed sources than in the single-plant scenario, in particular for low to intermediate values of the sensitivity $b$ to seed density. On the contrary, for high values of $b$ and intermediate values of $e$ the presence of several plants can be detrimental.
for the formation of hump-shaped patterns. Panels b, d and f of Fig. 4 evidence that overlapping seed shadows can remarkably alter the shape of the J–C region in the parameter space (β, α), but confirm that the presence of multiple seed sources can promote the establishment of J–C patterns, in particular for low to intermediate values of the plant fecundity α. On the contrary, the presence of overlapping seed shadows with very high fecundities α can have a negative impact on the formation of J–C patterns. This effect can be attributed to predator satiation (Nathan and Casagrandi, 2004). Overall, Fig. 4 shows that forest geometry has a limited impact on the establishment patterns produced by seed predation.

3.3. The role of social interactions among predators

It has already been shown that purely density-responsive seed foragers can generate hump-shaped establishment patterns in the case of congregation among conspecifics (Mari et al., 2008). In the context of CPF, congregating predators must be thought of as animals that tend to group independently of the fact that they share a nest. Therefore, the simplest way for analyzing the outcomes of attraction among conspecifics under density-dependent CPF is to use the following expression for the habitat suitability function:

\[ f(x, y, t) = bS(x, y, t) - eh(x, y) + cN(x, y, t), \]

where c represents the sensitivity to the local density of conspecifics. Note that if \( c < 0 \) predators repel each other. Top panels of Fig. 5 report one simulation of model (1)–(2) with habitat suitability function (6) in the single-plant scenario. The parameter setting used in the simulation is the same as in the top panels of Fig. 1, except for \( c > 0 \). Interestingly in this case, seed predation exerted by congregating foragers results in a monotonically decreasing radial distribution of seed density (panel c), while non-social foragers produced a J–C pattern (Fig. 1c). This result is due to the fact that attraction among conspecifics can significantly increase the clumping of predators around their nest, thus in turn affecting the spatial distribution of seed densities. Specifically, for this parameter setting, congregation and attraction to the nest operate synergistically and produce an extremely clumped distribution of seed predators (panel b).

The habitat suitability function (6) is the simplest, but not the only way to introduce social interactions among predators into our modeling framework. It specifically describes predators that are directly attracted \((c > 0)\) or repelled \((c < 0)\) by nestmates independently of their current activity. However, in the context of seed predation, attraction towards conspecifics may be related to a greater efficiency in locating food items. In other words, predators are attractive [repulsive] for nestmates depending on their success as foragers, i.e., in finding seeds [local enhancement [inhibition], see Section 1]. A simple way for introducing these features into the model is to assume that predators are sensitive to the number of foraging events per unit time in a specific location. This is given by the product between the predator’s functional response \(\psi(S)\) and the local density of seed foragers \(N(x, y, t)\). The resulting habitat suitability function can be written as

\[ f(x, y, t) = bS(x, y, t) - eh(x, y) + gS(x, y, t), \]

where \( g \) is a constant parameter representing the sensitivity to predation events. Note that Eq. (7) accounts for the local enhancement effect if \( g > 0 \), while the same equation describes local inhibition if \( g < 0 \). Bottom panels of Fig. 5 show a simulation of model (1)–(2) in which social interactions are mediated by successful predation events according to habitat suitability function (7). The parameter setting used in the simulation is the same as in the bottom panels of Fig. 1, except for \( g > 0 \). In this case, seed predators that take advantage of local enhancement to forage more efficiently produce a J–C recruitment pattern (panel f), while for the same parameter setting predation exerted by non-social predators \((g = 0)\) resulted in a monotonically decreasing pattern (Fig. 1f). Therefore, social interactions mediated by local enhancement can promote the formation of J–C patterns, at least for the parameter settings we have explored.

To better understand the role of congregation and local enhancement in the formation of establishment patterns we have performed the analysis of the model outcomes in the behavioral parameter space \((b, e)\) for different values of the parameters \( c \) and \( g \) (Fig. 6) and contrasted it to the results obtained with non-social foragers (the dashed curves in each panel of Fig. 6 mark the boundaries of the J–C region in Fig. 2a). Fig. 6a shows that congregation \((c > 0)\) causes a remarkable reduction of the J–C region in the parameter space \((b, e)\) with respect to the...
Fig. 6. Patterns generated by model (1)–(2) with the habitat suitability functions (6) (top panels) and (7) (bottom panels) and one single seed source for different choices of parameter settings and different social interactions among nestmates. White, light gray and dark gray regions mark parameter combinations leading to monotonically decreasing, J–C or Exact Compensation patterns. Dashed curves represent the boundary of the J–C region in the case of non-social predators (Fig. 2). Parameter values: (a) $c = 0.5$ (congregation); (b) $c = -0.5$ (repulsion); (c) $g = 1$ (local enhancement); (d) $g = -1$ (local inhibition). Simulation details as in Fig. 2.

We have also repeated the analysis of social interactions in the multiple-plants scenario. To contrast the results obtained with social foragers to those already described in the case of non-social predators, we have assumed the random forest geometry of Figs. 3 and 4. Fig. 7 shows that congregation (panel a) produces only a slight reduction of the J–C region for high values of sensitivity to distance from the nest and a small increase for intermediate e's, compared to the scenario in which seed predators do not have social interactions (dashed line). Repulsion among nestmates (Fig. 7b) leads to the opposite outcomes (the J–C region is larger for high values of sensitivity to distance from the nest and smaller for intermediate e's). Interestingly, local enhancement and inhibition (panels c and d, respectively) have a much stronger effect on the size of the J–C region in the parameter space (b, e). Specifically, local enhancement in a landscape with overlapping seed shadows allows seed foragers with a very low sensitivity to distance from their focal activity place to produce J–C patterns. On the contrary, local inhibition results in a remarkably smaller J–C region for low to intermediate values of e. Contrasting Fig. 6 to Fig. 7 shows that the J–C region in the parameter space (b, e) is always larger in the multiple-tree scenario than in the single-plant case. Congregation (panels a of Figs. 6 and 7) and local enhancement (panels c) lead to the most notable outcomes. Specifically, the presence of overlapping seed shadows favors the formation of J–C patterns for low values of (i) sensitivity to seed density in case of congregation or (ii) distance from the nest in case of local enhancement. These findings confirm the general idea that social interactions among conspecific foragers can alter spatial establishment patterns in a nontrivial way.

Finally, Fig. 6 and 7 show that different social interactions can produce similar results. For instance, both local enhancement and repulsion among nestmates can promote J–C patterns. However, the underlying mechanisms originating these similar outcomes are different. In fact, local enhancement highly increases the predators' ability to find food items, thus raising the efficiency...
of seed foraging. Instead, repulsion counters the clumping of predators around the nest due to distance-dependent effects, thus allowing foragers to explore larger areas than in absence of social interactions. The result that local enhancement can strongly promote the formation of J–C patterns is of particular interest per se. This social mechanism is in fact widely used by some of the most active post-dispersal seed predators, including harvester ants (see Section 1). However, although local enhancement is probably more common than simple congregation in the context of seed predation under CPF, we remark that both mechanisms (along with local inhibition and repulsion) can play an important role in determining the spatiotemporal patterns of social seed foraging.

4. Discussion and conclusions

We have extended here the mechanistic model for post-dispersal seed predation of Mari et al. (2008) to account for CPF, i.e., for seed predation due to foragers with a focal activity place distinct from the seed source. To describe seed foraging under CPF more realistically we have cast the model in a 2D landscape and introduced multiple seed sources with overlapping seed shadows. We have analyzed density-dependent predation and the effects of social interactions among foragers. In particular, we have investigated how different predators’ movement strategies can result in qualitatively different seed establishment patterns and specifically derived the conditions that lead to the formation of hump-shaped J–C patterns, which represent an important spacing mechanisms in forest ecosystems. A general result obtained from the analysis of our model is that J–C patterns can be found under wide ranges of ecological and environmental conditions, represented as different model parameterizations, forest geometries and predators’ movement strategies (Table 1).

In this work we have focused on CPF as a mechanism leading to pattern formation in forest ecosystems. However, plant-consumer interactions mediated by seed dispersal and predation are also key to the maintenance of the diversity of plant communities. In fact, the more common a species is in the ecosystem, the more its propagules suffer from predation by species-specific consumers (Janzen, 1970). Post-dispersal seed predation can thus induce frequency-dependent mortality, which is a well-known coexistence mechanism (Armstrong, 1989; Chesson, 2000). Convincing experimental evidence confirms that population-scale negative frequency dependence due to seed predators, seedling foragers or pathogens is crucial to the maintenance of high species diversity in both tropical and temperate ecosystems (Wills et al., 1997; Harms et al., 2000; Wills et al., 2006; Petermann et al., 2008). Janzen (1970) and Hubbell (1980) envisaged a direct role for the J–C pattern as a driver of the diversity of forest ecosystems. According to their reasoning, hump-shaped patterns should reduce recruitment near trees of the same species, thus promoting the establishment of other species. However, subsequent theoretical studies showed that J–C patterns, which represent just one of the possible local outcomes of seed predation (McCanny, 1985), are not

![Fig. 7. As in Fig. 6, in the case of multiple seed sources (random forest geometry, mean plant-to-nest distance equal to 10). White, light gray and dark gray regions mark parameter combinations leading to monotonically decreasing, J–C or Exact Compensation patterns. Dashed curves represent the boundary of the J–C region in the case of non-social predators and multiple seed sources with the same forest geometry. Parameter values and simulation details as in Fig 6.](image-url)
necessary to induce frequency-dependent mortality and promote species coexistence (Becker et al., 1985). Recent theoretical works have also shown that in some cases J–C patterns can even weaken the strength of frequency-dependent processes at the population level, thus potentially resulting in reduced biodiversity (Adler and Muller-Landau, 2005; Muller-Landau and Adler, 2007). In any case, J–C patterns are of paramount importance for determining the spatial arrangement of vegetation patterns in forest ecosystems.

We have tested whether our results are robust to changes of some of the modeling assumptions introduced in Section 2. In particular, we have repeated the analyses using different functional responses (Holling type I and type III) and alternative seed dispersal kernels drawn from the family of the exponential functions, which includes both thin- (e.g., Gaussian) and fat-tailed kernels (Clark et al., 1998). We have found that in the parameter ranges explored the predator’s functional response has little or no influence on seed predation patterns. More interestingly, we have observed that the shape of the seed dispersal kernel can have some impact on the emerging recruitment patterns, at least for large deviations from the reference exponential case (characterized by a shape parameter equal to 1 in the framework proposed by Clark et al. 1998). Specifically, Gaussian kernels (shape parameter equal to 2) seem to promote the formation of J–C patterns, while fat-tailed kernels (e.g., with a shape parameter equal to 0.5) are detrimental for the emergence of such patterns, in particular for low values of predators’ sensitivity to resource density. The J–C pattern is in fact produced by seed overexploitation in the proximity of the seed source (Nathan and Casagrandi, 2004). This condition seems to be favored if seeds are dispersed according to a Gaussian kernel (ceteris paribus, less seeds are in fact dispersed close to the parent plant with a Gaussian than with an exponential kernel) and unfavorited with a fat-tailed kernel of the exponential family (more seeds are dispersed close to the source).

Linking the outcomes of a simple – yet mechanistic – model like that presented in this work to experimental data could indeed provide ecologists with a deeper insight into the processes that govern seed establishment and, in turn, shape spatial vegetation patterns. However, field studies on central-place seed foraging as a determinant of vegetation patterns are quite rare and still at the frontier of the research on plant-animal ecology. In one of the best examples to date, Avgar et al. (2008) reported their experiments with two harvester ant species, Messor ebunius and M. arenarius. Both ant species are central-place foragers. While M. arenarius ants are solitary seed predators, M. ebunius use local enhancement (mediated by pheromonic cues) to inform and direct nestmates to spatial locations with high resource densities. Avgar et al. (2008) empirically showed that J–C patterns can be generated by seed predators that do not have their focal point at the seed source. They also found that differences in the foraging behavior of the two ant species result in qualitatively different seed establishment patterns. Specifically, they reported that the social ant M. ebunius does typically produce J–C establishment patterns, while the solitary ant M. arenarius does not. The findings that CPF and social foraging can result in J–C patterns give provide an interesting – though qualitative – support to our theoretical study.

From a quantitative perspective, a formal validation of our model could be rather complicated. In fact, although all model parameters are of easy interpretation, some of them would prove difficult to estimate. As noted by Holyoak et al. (2008), this should be particularly true for the quantities that describe directed movement (i.e., taxis coefficient and the parameters of the habitat suitability function). There are a few models in the literature that include the description of predators’ movement strategies and that have been tested in the field. Most interesting is the case of canid home range patterns (Moorcroft et al., 1999, 2006). Using a mechanistic PDE model, Moorcroft and colleagues were in fact able to relate the movement behavior of coyote populations with the resulting spatial distribution. Social interactions among predators are expected to be difficult to parameterize as well. To this purpose, relevant to our analysis is the work by Grünbaum and Veit (2003), who proposed and tested a spatially implicit, ordinary differential equation model for predator-prey interactions between albatrosses and Antarctic krill and tried to evaluate the relative importance of resource and conspecific abundances in orienting predators’ movement.

Future developments of our research will regard a better description of predators’ movement strategies, so as to increase the realism of the model. The flexibility of our approach could be used to study some interesting problems related to post-dispersal seed predation, such as the competition of two or more species of central-place foragers characterized by different movement behavior. Introducing multiple predators’ nests would be of great biological interest, in particular in the case of overlapping seed shadow. In fact, the model in its present form can be rigorously applied to single-nest (monodomic) seed foragers that do not suffer from interspecific competition or predation, while polydomic species and interspecific interactions can be less effectively accounted for in our simple framework. From a purely mathematical perspective, extending the model to the case of multiple nests would be straightforward, only requiring a slight modification of the seed equation (to account for predation by foragers of different nests) and the introduction of one replica of the predator equation for each nest. However, from an ecological viewpoint, the analysis of the multiple-nest case is expected to be fairly complex. The first source of complexity is technical and concerns the definition of the spatial distribution of nests, which does obviously reflect long-term trends of resource availability, intra/interspecific competition and predatory pressure (see Hölldobler and Wilson, 1990, for a discussion regarding harvester ants). The second problem is more profound and deals with the description of social interactions among foragers living in different nests and potentially, yet not necessarily, belonging to different forager species. In this case the spectrum of possible interactions would become remarkably larger, including inter-nest or interspecific competition and/or facilitation. Although rather complex, all these extensions are certainly interesting and worth future investigations, because they would allow the application of the model to species-specific cases, such as that of harvester ants.

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