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LETTER

Linking traits of foraging animals to spatial patterns of plants: social and solitary ants generate opposing patterns of surviving seeds

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Abstract

Foraging traits of seed predators are expected to impact the spatial structure of plant populations, community dynamics and diversity. Yet, many of the key mechanisms governing distance- or density-dependent seed predation are poorly understood. We designed an extensive set of field experiments to test how seed predation by two harvester ant species interact with seed dispersal in shaping the spatial patterns of surviving seeds. We show that the Janzen–Connell establishment pattern can be generated by central-place foragers even if their focal point is located away from the seed source. Furthermore, we found that differences in the social behaviour of seed predators influence their sensitivity to seed density gradients and yield opposing spatial patterns of surviving seeds. Our results support the predictions of a recent theoretical framework that unifies apparently opposing plant establishment patterns, and suggest that differences in foraging traits among seed predators can drive divergent pathways of plant community dynamics.

Keywords

Density dependence, foraging strategy, harvester ants, Janzen–Connell hypothesis, plant recruitment, seed dispersal, seed predation, social behaviour, spatial patterns.

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INTRODUCTION

The spatial pattern of dispersed seeds (i.e. the seed shadow) forms the initial template for plant establishment, a pattern which is progressively reshaped by both abiotic and biotic factors (Nathan & Muller-Landau 2000). Because mortality in plants occurs chiefly between dispersal and germination stages (Harper 1977), processes operating at this juncture, most notably post-dispersal seed predation (Janzen 1970; Hulme 1998), can shape the spatial structure of plant populations (Augspurger & Kitajima 1992). Because of their importance in determining spatial population structure, seed predators (and seedling herbivores) may play a crucial role in maintaining high species diversity in plant communities (Janzen 1970; Connell 1971).

The Janzen–Connell (J–C) hypothesis asserts that distance- or density-dependent seed predation, or seedling herbivory, decrease conspecific establishment at the proximity of the seed source, thus generating a hump-shaped pattern of peaked establishment at some intermediate distance away from the seed source. However, this particular pattern is only one of five possible establishment patterns – each constituting a qualitatively unique combination of dispersal and survival (Nathan & Casagrandi 2004) – that can be generated by distance-dependent dispersal and predation (McCanny 1985). For example, Hubbell (1980) predicted a monotonically declining establishment pattern, despite a distance-dependent increase in survival, because of disproportionately high seed density at the vicinity of the seed source. McCanny (1985) suggested a rapidly declining establishment pattern resulting from decreasing survival with distance from the seed source, which may occur, for instance, when seed predators are saturated close to the seed source. These two patterns, together with an invariant survival pattern, are monotonically declining and are thus qualitatively distinguishable only via a mechanistic examination of the seed survival process (Nathan & Casagrandi 2004). Although these different patterns were considered to represent conflicting processes, they can all be produced by distance-dependent dispersal and predation, and thus constitute specific cases along a continuum ranging from the J–C pattern at one extreme to the McCanny pattern at the other extreme (Nathan & Casagrandi 2004).

Nathan & Casagrandi (2004) showed that the scale parameters of dispersal and predation (i.e. the mean distance of dispersed seeds and seed predators, respectively, from the seed source) interplay to determine the establishment curve. In particular, quantitative differences in one or more foraging traits of seed predators were shown to give rise to qualitatively different establishment patterns (see their Fig. 5). Thus, the foraging characteristics of seed predators may help explain and predict the spatial structure of plant populations and the potential for maintaining high diversity in plant communities. Remarkably, despite four decades of extensive research stimulated by Janzen's (1970) ideas, that link plant spatial patterns to animal foraging, the most fundamental interaction of this link – between seed shadow properties and predator foraging strategies – has not yet been empirically investigated until now.

Ants, major seed predators in many ecosystems (Gordon 1993; MacMahon *et al.* 2000; Albert *et al.* 2005), may play a crucial role in determining the spatial structure and composition of plant populations (Orrock *et al.* 2006). Density-dependent seed predation by ants results in disproportionately high seed mortality in dominant plant species, thus allowing proximate subordinate species to survive, and leads to relatively high plant diversity at the vicinity of ant nests (Guarino *et al.* 2005). The foraging strategies of seed-eating ants may vary in many aspects, including functional response, nestmate recruitment, spatial and directional fidelity, use of long or short-term memory, reaction to environmental cues and spatiotemporal flexibility (Davidson 1977; Traniello 1989). Of particular importance is the variation associated with information-sharing among nestmates during foraging, with solitary foraging at one extreme and mass-recruitment (social) foraging at another. Experimental and theoretical studies have shown that socially foraging ants are more efficient in utilizing clumped resources while solitary foragers are more efficient when resources are scattered (Davidson 1977; Johnson *et al.* 1987; Jaffe & Deneubourg 1992).

The performance of seed predators as optimal foragers depends on their efficiency in detecting new seed patches and in utilizing detected patches (Hulme 1993). These traits often exhibit a trade-off associated with differences in information-sharing behaviour. In ant communities, this trade-off is often played along a sociality axis with solitary foragers expected to be more efficient detectors and less efficient utilizers than social foragers (Davidson 1977; Fellers 1987).

To the best of our knowledge, the present study is the first to empirically examine how seed predators that differ in their foraging traits affect the establishment patterns of plants. Specifically, we present an extensive set of field experiments designed to investigate how seed predation by two sympatric harvester ant species, *Messor ebeninus* Forel and *Messor arenarius* Fabricius, subjected to different seed shadows, affect the spatial patterns of surviving seeds. We selected these two ant species because of the marked differences in their foraging strategies. *Messor ebeninus* has large colonies (*c.* 10^5 individuals) and is a highly social forager, which uses pheromonal cues to inform and direct nestmates to specific sites of high-density resources (Steinberger *et al.* 1991). *Messor arenarius* has much smaller colonies (*c.* 10^3 individuals) and is considered a solitary forager, which exhibits a high degree of patch-fidelity at the individual level (Warburg 1996). We hypothesize that these characters will result in a species-specific effect on the spatiotemporal distribution of seeds surviving predation (i.e. the potential establishment pattern). More specifically, we predict that due to its mass-recruitment behaviour, the social forager *(M. ebeninus)* will focus its foraging activity at the core of the seed shadow (where seed density is highest), thus shift the median and the mode of the seed shadow and generate a hump-shaped pattern of surviving seeds, consistent with the J–C model. In comparison, the solitary forager *(M. arenarius)* is expected to be less sensitive to the seed density gradient, thus have little effect on the median and mode of the original seed shadow, generating a monotonically declining potential establishment pattern. Our results clearly support this hypothesis and show that socially and solitary-foraging ants generate, respectively, hump-shaped and gradually declining potential plant establishment patterns.

METHODS

Field experiments were conducted in the 'Sayeret-Shaked' Park in the north-western Negev Desert, Israel (31°16′34.44″N, 34°39′7.69″E). The park is an arid shrubland with a few dominant perennial shrubs (Wilby & Shachak 2004) and two dominant invertebrate seed predators*:* *M. ebeninus* and *M. arenarius* (Avgar 2007).

During January 2006, we isolated two colonies of each species in a large circular enclosure (20 m radius) with a 20 cm high polypropylene multiwall sheet (Avgar 2007). We evaluated the efficiency of the barrier by placing seeds in small quarantined test arenas, from which no seed loss was observed during the study. We generated an artificial isotropic seed shadow within each enclosure with a peak at a distance of 10 m from the nest entrance, using the following procedure: 225 shallow depressions ('patches') were created in a 15 × 15 m grid; in each patch seeds were protected from vertebrate granivory by a plastic cage placed above the patch (Fig. 1). To minimize the effect of the natural seed flow on the foraging behaviour of the experimental colony, we used rice seeds whose energetic content is much higher than that of any local seed and are

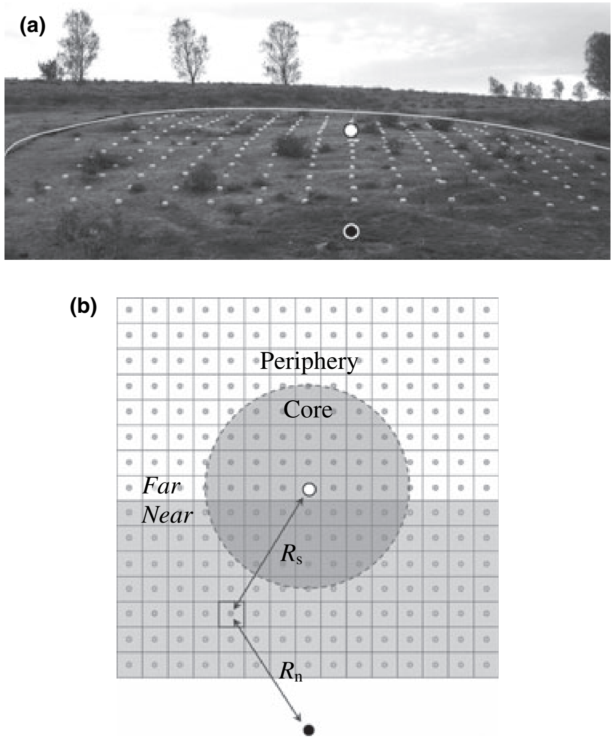

Figure 1 The experimental setup. (a) The centre of the 15 × 15 m patch array (white circle) was positioned 10 m from the ant nest (black circle). Each patch was protected from vertebrate granivory by a plastic cage (white squares). The nest and the patch array were quarantined in a 20 m radius circle by a 20 cm high polypropylene multi-wall sheet (white line). (b) A scheme of the experimental setup: seeds were placed in a small depression (grey dots) in the middle of each 1 × 1 m grid cell. The centre of the artificial seed shadow (white circle) is located 0.5 m from the *Near-Far* boundary, 4.3 m from the core-periphery boundary and 10 m from the ant nest (black circle). R_s and R_n are the distances of seed patches from the centre of the seed shadow and the nest, respectively.

thus strongly preferred by the ants. The number of rice seeds in each patch was set daily according to its distance from the centre of the array, following a two-dimensional negative exponential seed dispersal kernel:

$$N(R_s) = \frac{2\alpha}{\pi D^2} e^{\left(-\frac{2R_s}{D}\right)}$$

where $N(R_s)$ is the number of seeds at distance R_s from the centre of the seed shadow, α is the daily fecundity and D is the scale parameter, which equals in this particular function the mean dispersal distance (Nathan & Casagrandi 2004).

At the dawn of each experimental day we exposed each isolated colony to an artificial seed shadow generated by dispersing $\alpha = 500$ rice seeds, according to a randomly chosen D value ($D = 0.5$, 2.5 or 5 m; Fig. 2, middle column). We repeated each colony-by-D combination several times for a total of 30 experiments (see Avgar 2007 for more details). We monitored the patches for seed loss every 0.5–3 h until dusk when ant foraging ceased. Throughout the experiments, ground temperature was recorded every 10 s by a TX thermocouple electrode connected to a data logger (21X; Campbell Scientific Inc., Logan, UT, USA).

In the initial exploration of the data, we found no intraspecific colony effect and therefore pooled the data for each species-by-D combination. We used a relative risk regression approach (Cox regression) to analyse seed detection and depletion data, assuming that seed predation events have some underlying basal rate (or hazard) from which the actual rate deviates according to the covariate values characterizing specific localities (Kalbfleisch & Prentice 2002). The model hazard function [$h(t)$] is of the following general form:

$$h(t) = [h_0(t)]e^{(B_1X_1+B_2X_2+\ldots+B_pX_p)}$$

where $h_0(t)$ is the baseline hazard function, X_1 to X_p are the covariates and B_1 to B_p are the coefficients of the covariates. We determined whether the species differ significantly in their sensitivity to the different covariates according to the maximum likelihood estimates of the 95% confidence bounds of the covariates coefficients.

Confidence bounds for the frequency of survival probabilities were computed according to Zar (1996, p. 524). To test for changes in the median and mode of the seed shadow following predation we used the percentile bootstrap method (Manly 1997). All statistical tests were performed in SPSS 14.0 (SPSS Inc., Chicago, MI, USA). Randomization tests where programmed in MATLAB R2007b (The MathWorks Inc., Natick, MA, USA).

RESULTS

Our experiments revealed considerable variation in the magnitude and the spatial pattern of seed predation in response to both dispersal scale (D) and the identity of the foraging species (Fig. 2). In the following sections, we describe a sequential set of analyses aimed at elucidating the major factors structuring such variable patterns of seed predation, and consequently the potential establishment patterns.

Patch detection

We begin by analysing patch detection time, defined as the time elapsed between the time the colony initiated foraging activity and the time the first seed was removed from the patch. Patches that were not detected until the end of the experiment were treated as censored data. Although the two species do not differ in their overall detection success

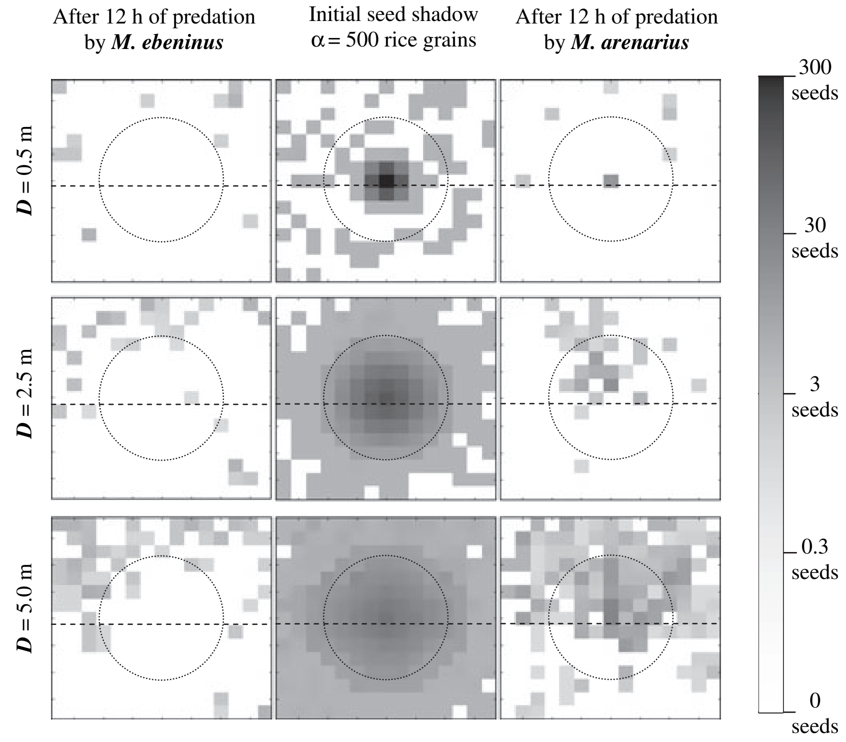

Figure 2 The experimental seed shadow for different mean seed dispersal distance (D, rows) before and after 12 h of seed predation by ants. Each map represents the 15 × 15 m patch array used for the experiments. Different shades of grey represent different seed numbers (in log scale). The ant colony is located 3 m below the lower edge of the array. The straight dashed line is the *Near-Far* boundary and the dotted circular line is the core-periphery boundary. The maps were produced by averaging all the experiments for each species-by-D combination.

(94%), *M. arenarius* is significantly faster in detecting new patches (*M. arenarius* median detection time = 77 min, $n = 1662$, *M. ebeninus* median detection time = 102 min, $n = 1652$; Mann–Whitney test, $Z = -4.9$, $P < 0.001$). We assumed a species-specific baseline hazard function and thus constructed relative risk regression models separately for each species, with the following covariates: patch distance from the nest (R_n), mean ground temperature (T_{gr}) and patch distance from the centre of the seed shadow [$R_s(D)$], which is independently evaluated for each D value by multiplying R_s by a dichotomous D dummy variable, thus creating three $R_s(D)$ covariates, one for each D value. For example, $R_s(2.5)$ equals the patch R_s value if its D value equals 2.5 and zero if $D \neq 2.5$.

The patch relative detection hazard increases with T_{gr} and decreases with R_n and this effect does not differ significantly between species (Table S1). R_s has a significant negative effect on the patch relative detection hazard. Hence, patches located closer to the seed source are more likely to be detected. We found no significant difference in the relative effect of R_s on patch relative detection hazard under different D values within the same species; yet the effect of R_s is significantly stronger in *M. ebeninus* than in *M. arenarius* (Fig. 3a).

Patch depletion

In the next step of our analysis, we focus on patch depletion time, defined as the time elapsed between the time the patch was detected and the time the last seed was removed from the patch. Undetected patches, or patches containing only one seed, were excluded from the analysis. Patches that were not depleted until the end of the experiment were treated as censored data. *Messor ebeninus* exhausts a higher percentage of detected patches than *M. arenarius* (97% vs. 86%, $\chi^2 = 27$, d.f. = 1, $P < 0.001$) but the two species do not differ in the median depletion time per seed (12 min). We used the same model structure as in the detection analysis with two added covariates: *Detection Time* (the time at which the patch was detected) and the initial number of seeds in the patch [$I_s(D)$], which is independently evaluated for each D value by multiplying I_s by a dichotomous D dummy variable.

The two species do not differ in the negative effects of R_n and *Detection Time* on their relative depletion hazard functions (Appendix Table S1). However, *M. arenarius* is significantly more sensitive to the positive effects of T_{gr} and R_s than *M. ebeninus* (Appendix Table S1). Patch relative depletion hazard decreases with I_s and D for both species (Fig. 3b). Therefore, the time needed to consume all the seeds in a patch increases with the initial seed number and this effect amplifies as the scale of the seed shadow increases (i.e. as the initial seed density gradient flattens).

Seed survival

Here we examine the product of the detection and depletion abilities of the two ant species, that is, the seed survival

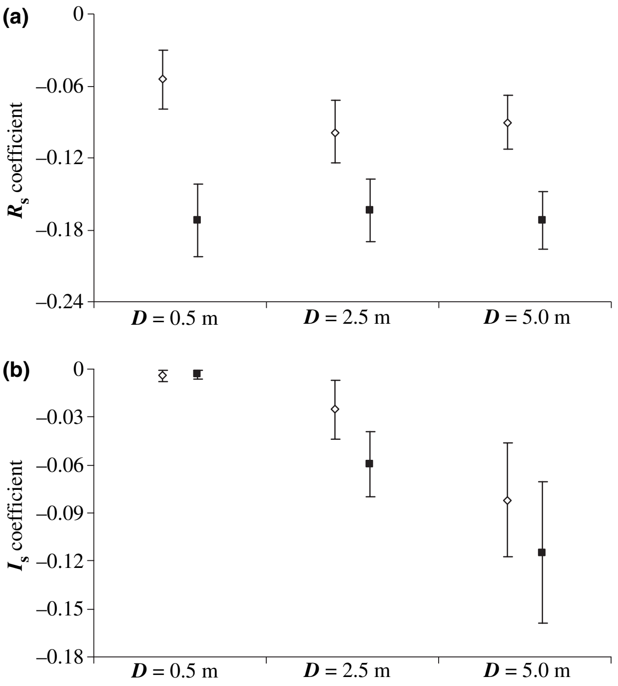

Figure 3 Maximum likelihood estimates of the Cox regression coefficients for the effects of (a) the distance from the centre of the seed shadow (R_s) on patch detection rate and (b) the initial number of seeds in a patch (I_s) on its depletion rate, by *Messor arenarius* (white diamonds) and *M. ebeninus* (black squares). Error bars represent 95% confidence bounds.

probability. Overall seed survival (ranging between 1% and 20%) is significantly higher for *M. arenarius* than *M. ebeninus* and it increases with D for both species (Appendix Fig. S1). We divide each experimental seed shadow into two parts: an inner circle ('core'; $R_s < 4.3$ m), constituting 25% of the array area, and an outer ring ('periphery'; $R_s > 4.3$ m; Figs 1b and 2). Recall that higher seed survival in the periphery of the seed shadow compared to its core is a required feature for both the J–C and the Hubbell patterns; whereas an opposite trend characterizes the McCanny pattern (see Introduction).

We found that seed survival is significantly higher in the periphery of the seed shadow, for all D values for *M. ebeninus*, and for D = 0.5 m and D = 2.5 m for *M. arenarius* (Table 1). However, for D = 5 m, *M. arenarius* does not generate a significant difference in seed survival between the core and the periphery (Table 1). A more detailed examination of the survival patterns reveals that both the magnitude and the decrease with D of the core-periphery difference in survival are considerably weaker for *M. arenarius* than for *M. ebeninus* (Table 1 and Fig. 4).

A seed predator with a limited foraging range, and whose activity centre is away from the seed source, may generate a one-dimensional pattern of increasing seed survival with R_s even without any response to either seed density or R_s (Avgar 2007). We tested for this side effect of R_n by repeating the core-periphery seed survival comparison separately for patches located in the array section closer to the nest (*Near*; the first 105 grid cells) and patches located in the section farther away from the nest (*Far*; the last 120 grid cells; Figs 1b and 2). If the increase in seed survival at high R_s is just a side effect of R_n, it should be reversed in the *Near* section, where R_s is mostly negatively correlated with R_n. *Messor ebeninus* generates significant increase in seed survival in the periphery of the seed shadow regardless of the array section (Table 1). However, for *M. arenarius*, higher seed survival in the periphery compared to the core was found only in the *Far* section, whereas no significant difference was found in the *Near* section for D = 0.5 m and D = 2.5 m and a significant reversed difference (higher survival in the core) was found for D = 5 m (Table 1).

In summary, we found that the probability of a seed to survive predation by *M. ebeninus* increases with the distance from the seed source (R_s) regardless of its correlation with R_n. The magnitude of this trend decreases with D (Fig. 4 and Table 1). The probability of a seed to survive predation by *M. arenarius* showed a much weaker increase with R_s for low D values, and was spatially invariant for high D values (Fig. 4 and Table 1).

Potential establishment patterns

In the last step of our analysis, we examine the ant-generated spatial pattern of surviving seeds (i.e. the potential establishment patterns). To enable comparison with the one-dimensional establishment patterns hypothesized and tested in nearly all published studies (Hyatt *et al.* 2003), we examine the ant-generated potential establishment densities along the R_s axis. The density of seeds surviving predation by *M. ebeninus* displays a hump-shaped pattern with its minimum at the core of the seed shadow (Fig. 4). For *M. arenarius*, the density of surviving seeds declines with R_s in a pattern that qualitatively mirrors the initial seed shadow with peak surviving seed density at the core of the seed shadow (Fig. 4).

As predicted, seed predation by *M. ebeninus* generates significant shifts in both the median and the mode of the seed shadow and the magnitude of these shifts decrease with D (Fig. 5). Thus, *M. ebeninus* generates a clear J–C pattern that becomes more pronounced as the scale of dispersal decreases. Seed predation by *M. arenarius* does not generate any significant shift in the median or the mode of the seed shadow (Fig. 5), thus conserving the initial pattern of declining densities of dispersed seeds, regardless of the seed dispersal scale.

Table 1 Seed survival in the core vs. the periphery of the seed shadow

Seed shadow section	D (m)	Species	Seed survival (%)		χ^2
			Core $R_s < 4.3$ m	Periphery $R_s > 4.3$ m	P-value
All	0.5	*Messor arenarius*	0.66	6.84	< 0.001
		M. ebeninus	0.00	20.92	< 0.001
	2.5	*M. arenarius*	3.08	6.38	0.004
		M. ebeninus	0.10	8.95	< 0.001
	5	*M. arenarius*	18.50	19.52	0.57
		M. ebeninus	0.38	12.84	< 0.001
Near	0.5	*M. arenarius*	0.00	0.00	
		M. ebeninus	0.00	4.35	0.001
	2.5	*M. arenarius*	0.17	0.70	0.26
		M. ebeninus	0.00	3.83	< 0.001
	5	*M. arenarius*	10.68	5.98	0.01
		M. ebeninus	0.23	2.95	0.002
Far	0.5	*M. arenarius*	0.73	12.12	< 0.001
		M. ebeninus	0.00	21.05	< 0.001
	2.5	*M. arenarius*	4.72	10.43	0.004
		M. ebeninus	0.15	11.11	< 0.001
	5	*M. arenarius*	23.31	33.41	< 0.001
		M. ebeninus	0.47	20.41	< 0.001

Near is the array section adjacent to the ant nest and *Far* is the opposite, more distant, section (see Figs 1b and 2). Seed survival is the probability (in %) of a seed to survive from dawn to dusk. Differences in seed survival between the core and the periphery were tested using two-sided χ^2 test with d.f. = 1.

DISCUSSION

Variation in the degree of sociality among foragers has been attributed to the well-documented trade-off between detection and utilization of food resources (Davidson 1977; Lebrun & Feener 2007), which is directly related to their efficiency in extracting sparse vs. clumped food items. We confirmed the existence of such a trade-off in our study system, and documented, for the first time, how the position of the seed predator along the trade-off axis affects the spatial patterns of surviving seeds. Our results support the general theoretical prediction of Nathan & Casagrandi (2004) that the dispersal characteristics of plants and the behavioural traits of seed predators interplay to determine potential plant establishment patterns. We also show that density-responsive seed predators may generate hump-shaped plant establishment patterns even if their focal point of activity is away from the seed source. This implies that a key assumption of the J–C model, requiring foragers to centralize their activity at the seed source, is not a necessary condition for the J–C pattern to occur.

The detection-utilization trade-off

The rate at which both ant species detect and deplete food resources depends on temperature and the distance of the patch from the nest, as can be expected for ectothermic, central-place foragers. Despite it's considerably smaller colony size, *M. arenarius* detects new seed patches significantly faster than *M. ebeninus*. Once seeds have been detected, *M. ebeninus* recruits massively and thus harvests seeds more rapidly. These findings confirm the expectations derived from previous studies (see Introduction) that solitary-foraging species are adapted to forage on sparse low-density food resources, requiring high detection abilities, whereas socially foraging species, which specialize on fast depletion of detected food patches, are more adapted to utilize clumped, high-density resources.

Foraging traits and plants spatial patterns

For both species, patch detection was found to be more probable near the centre of the seed shadow (high seed densities) than farther away from it (low seed densities). However, *M. arenarius*, the solitary-foraging species, is significantly less sensitive to this density gradient than *M. ebeninus*, the social forager (Fig. 3a). The probability of depleting a detected patch declines with the number of seeds in that patch, and this effect intensifies with the scale of the seed shadow (Fig. 3b). For *M. ebeninus*, the density of seeds surviving predation in the core of the seed shadow increases from zero to *c.* 0.01 seeds m^{-2} with an increase in

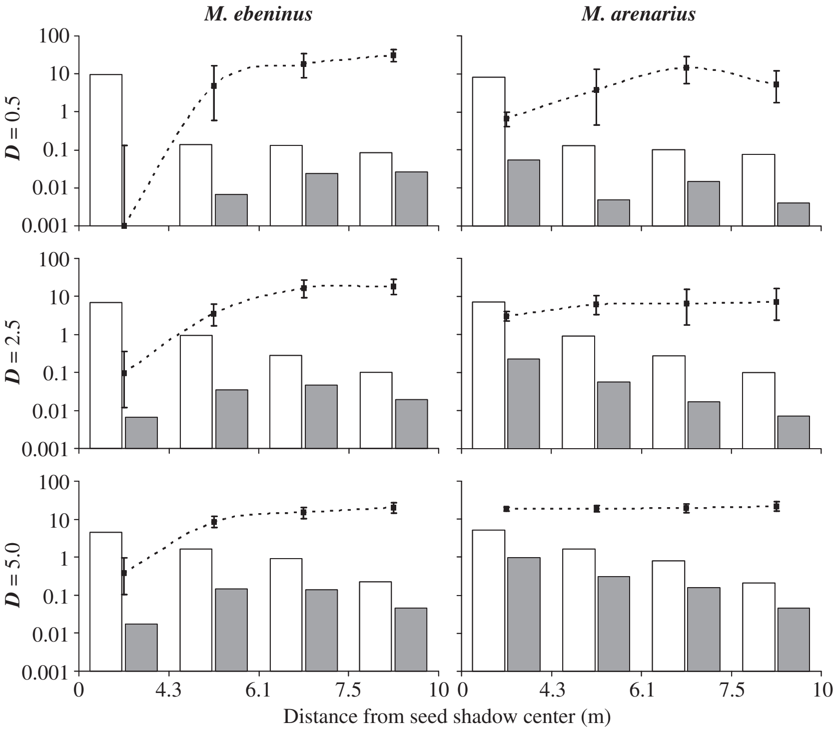

Figure 4 Semi-log plots of initial densities of artificially dispersed seeds (seeds m^{-2}; white), seed survival (%; dashed line) and densities of seeds surviving predation (seeds m^{-2}; grey) in equal-area (57 m^2) categories of the distance from the centre of the seed shadow. The first (shortest distance) bin corresponds to the core of the seed shadow discussed in Table 1. Bars represent 95% confidence bounds.

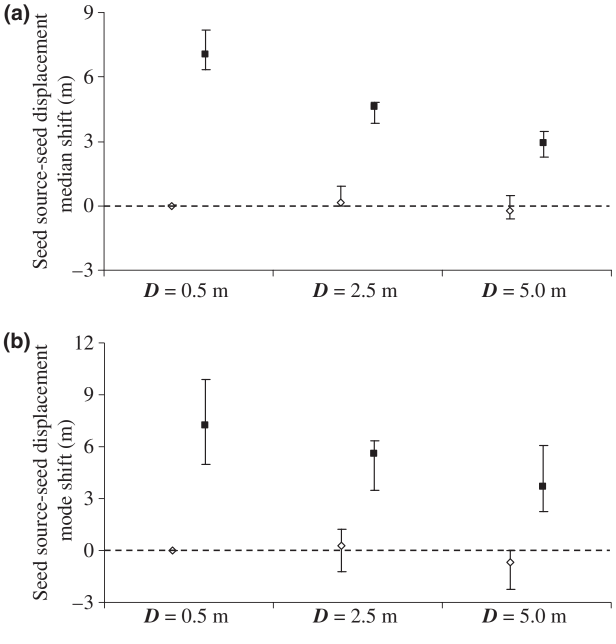

Figure 5 The shift in (a) the median and (b) the mode of the seed shadow (the distances between the seeds and the seed source) during a day of predation by *Messor arenarius* (white diamonds) and *M. ebeninus* (black squares). Error bars represent bootstrap estimates of 95% confidence bounds. The dashed line marks zero difference; that is, no shift in the distribution.

D (thus reversing the trend of the initial seed density; Fig. 4) and the shift in both median and mode of the seed shadow increases with a decrease in *D* (i.e. as the initial seed density gradient increases; Fig. 5).

These findings imply that on the colony level, both species, and especially the social forager, react not only to the local seed density but also to the density gradient. These observations are compatible with a weak positive density-dependence effect resulting from patch fidelity in *M. arenarius* and a much stronger effect due to mass recruitment in *M. ebeninus*. This difference between the two ant species in their sensitivity to the seed density gradient provides the means to qualitatively test the theoretical predictions made by the general model of Nathan & Casagrandi (2004).

Nathan & Casagrandi (2004) concluded that the scale parameters of dispersal and predation (*D* and *q*, respectively) interplay to determine plants establishment patterns (see Introduction). Although not explicitly quantified, our results indicate that *q* is strongly affected by the foraging strategy of seed predators and thus is an important characteristic of seed predation patterns, even when seed predators are not centred at the seed source. *Messor arenarius* and *M. ebeninus* differ in their foraging strategy and therefore generate qualitatively different survival and potential establishment patterns (Fig. 4). Specifically, the social forager, *M. ebeninus*, tends to aggregate where seed density is highest, and is thus highly sensitive to the distance from the centre of the seed shadow (i.e. relatively low q value). *Messor arenarius* is less sensitive to the density gradient and, thereby, to the distance from the centre of the seed shadow (i.e. high q value). As hypothesized, and in concordance with the Nathan & Casagrandi (2004) predictions (see their Fig. 5), *M. ebeninus* generates a hump-shaped (J–C) pattern, while *M. arenarius* tends to generates a gradually declining potential establishment pattern (Figs 2, 4 and 5).

The sensitivity and response of seed predators to the seed shadow (i.e. R_s or I_s) may be species-specific (as in the case of the differential R_s effect on detection hazard; Fig. 3a) and/or dispersal-scale dependent (as in the case of differential I_s effect on depletion hazard; Fig. 3b). These various facets of sensitivity to attributes of the seed shadow are predictably translated into variation in the generated patterns of seed survival.

Seed enemies need not be at seed source: relaxing a key J–C assumption

An underlying assumption of the J–C hypothesis is that seed predators originate at the centre of the seed shadow (Janzen 1970; Nathan & Casagrandi 2004). However, this assumption rarely holds for birds, rodents and ants, the dominant post-dispersal seed predators in most ecosystems (Hulme & Kollmann 2004; Fenner & Thompson 2005). Previous investigations of the J–C hypothesis have often ignored the question of the relative location of the focal point of seed predators (Hyatt *et al.* 2003). Yet, evidence in support of the density- and/or distance-dependent seed survival, as predicted by the J–C hypothesis, has been found in many studies involving seed predators whose centre of activity is unlikely to coincide with the seed source (Platt 1975; Augspurger & Kitajima 1992; Hulme 1998; Nathan *et al.* 2000; Wyatt & Silman 2004). In our experimental setting, the location of the centre of ant activity (i.e. the ant nest) was unambiguously outside the experimental seed shadow (Fig. 1). Despite the relatively large distance between the ant nest and the seed source (larger than the maximum dispersal distance of seeds), and the fact that ants search for seeds on the ground and, unlike birds, cannot 'jump' to the centre of the seed shadow, we found a clear negative effect of the distance from the centre of the seed shadow on detection, depletion and, consequently, on predation probability of dispersed seeds. We thus explicitly show that the J–C pattern may arise even when ground-dwelling seed predators are centred away from the centre of the seed shadow, and also provide a behavioural mechanism that explains why this key assumption can be relaxed. In monotonically declining seed shadows, the distance from the centre is a strong indicator for seed availability, and thus the initial spatial structure of seed density directs the predators towards the centre of the seed shadow.

Although the J–C model requires predators to be host-specific, the major seed-eating guilds are generalists. However, in many ecosystems, generalist seed predators may be facultative host-specific due to spatiotemporal variations in seed availability (Janzen 1970). Seasonal diet shift compatible with the concept of facultative host-specificity has been observed for both *M. arenarius* and *M. ebeninus* in our study area (Wilby & Shachak 2000).

In addition to ants, socially foraging seed predators that may generate a J–C establishment patterns may include beetles (Honek *et al.* 2005), flocking birds (Kelt *et al.* 2004) and large mammals (Wyatt & Silman 2004) that may operate at much larger spatial scales. However, seed predation at the vicinity of the seed source may also be influenced by the predation risks associated with canopy cover, cryptic seeds and mobility limitations (Wilby & Shachak 2000; Walther & Gosler 2001; Fenner & Thompson 2005).

Pros and cons of our experimental approach

The spatiotemporal patterns of seed predation can tremendously impact plant communities (Janzen 1970; Borchert & Jain 1978; Goldberg 1985; Hulme 1998), but elucidating the specific key factors responsible for this relationship is a challenging task. We approached this challenge by experientially controlling the key factors (seed shadow characteristics and behavioural traits of seed predators) and minimizing noise from other potential factors and more complex interactions (e.g. seeds of other species, other seed predators, overlapping seed shadows, overlapping ant colony foraging ranges). As with all experimental manipulations, the major pro is the potential to clearly elucidate how specific key factors drive the focal process under study. This merit has enabled us to show unequivocally that differences in foraging traits among two harvester ant species interact in a predictive manner with seed shadow characteristics to produce different spatial patterns of seeds surviving predation. Because of the experimental manipulations, our study is unique in examining the effects of seed predation in a detailed two-dimensional density gradient of dispersed seeds, and, most importantly, in explicitly elucidating the importance of foraging characteristics of seed predators. Disregarding these aspects, as has been done in many previous works (e.g. Hyatt *et al.* 2003), may lead to misinterpretation of observational and experimental results.

However, important insights and mechanistic understanding of the problem must always be evaluated considering the cost of over-abstraction of reality. In the following, we address some cons of our experimental approach, and their implications for the interpretation of the results, as well as recommendations for future attempts to close some possible gaps between our experiments and reality.

To discern a unique predator–prey system, we isolated single ant colonies and used highly energetic rice grains rather than naturally occurring seeds. Ant attraction to rice seeds negates the effects of the natural flow of seeds into the experimental area, and sterilization of such relatively large area from any natural seed flow is practically impossible. Moreover, as our main interest was in comparing the two study species, we were obliged to provide both with exactly the same resource. It may be argued that the use of rice grains changes the natural behaviour of the seed predators. However, because harvester ants store collected seeds, the colony is rarely saturated and its foraging behaviour is affected mainly by the microclimatic conditions (Azcarate *et al.* 2007) and the density of the resource (Crist & MacMahon 1992) rather than its energetic yield. Those conducting future manipulative studies may wish to use native seeds in a sterile area, but the complications involved in such an effort and the uncertainty about its effects on animal foraging behaviour should always be kept in mind. A potentially promising approach, admittedly much more demanding, is to mark naturally dispersing seeds and observe their detection and depletion with time.

Quarantining single ant nests, which prevents ants of other colonies and species from foraging in the same area, generated an artificial isolation of foraging strategies that departs from the frequent observation of sympatric coexisting seed predators (Johnson 2000). However, if we wish to understand how different seed predators jointly shape post-dispersal seed patterns, we need to understand the forces that affect the relative abundance and performance of different foraging strategies (Glasser 1979). These may include the distribution patterns of the resources themselves (Gordon 1991; McGlynne & Kirksey 2000; Silverman & Roulston 2003), physical conditions such as temperature (Delsinne *et al.* 2007), and biological factors such as natural enemies (Weier & Feener 1995) and the introduction of invasive species (Human & Gordon 1996).

Similarly, the seed shadows of conspecific plants often overlap (Nathan & Muller-Landau 2000). Thus, the seed density gradients on which predators operate are seldom as simple as the artificial seed shadows in the present experiments. Nevertheless, we believe that the clear finding of species-specific sensitivity to seed density gradients represents the fundamental 'rule-of-thumb' response of ants to the distribution of their resources, regardless of the degree of overlap among neighbouring seed shadows.

Finally, we must keep in mind that the pattern of surviving seeds quantified in our study may not accurately correspond to the long-term establishment pattern, although the underlying mechanisms are likely to operate similarly throughout the dispersal season. Furthermore, post-dispersal seed predation is only one of several processes affecting plant establishment patterns and the relative importance of these processes will determine the effects of the foraging strategy of seed predators on the spatial structure of plant populations.

CONCLUSIONS

Using an extensive set of field experiments, we showed complex relationships between foraging traits of animals and the spatial patterns of seed survival, which can determine plant spatial population structure, and subsequently community dynamics and diversity.

In isolation, a social forager such as *M. ebeninus* is expected to significantly reduce seed survival at the vicinity of adult plants during the dispersal season and promote the coexistence of plant species via a Janzen–Connell process. A solitary-foraging seed predator such as *M. arenarius* is expected to leave behind relatively high densities of seeds in the vicinity of the mother plant, thus qualitatively conserving the initial pattern of declining densities of dispersed seeds and, consequently, generate clumped distribution of conspecific.

Indeed, the J–C process may play an important ecological and evolutionary role not only in the tropics, but in many other ecosystems (e.g. Nathan *et al.* 2000; Hyatt *et al.* 2003). Our results highlight the need to investigate the effects of different foraging strategies, and specifically the level of sociality and information sharing, on spatiotemporal patterns of prey abundance, because these may have tremendous effects on many ecological processes. Future work should focus on theoretical and experimental investigation of more complex representations of spatial seed predation patterns: different distances between the focal point of the seed predators and the centre of the seed shadow, multiple and overlapping seed shadows, multiple and competing seed predators and differential energetic gains/costs of dispersed seeds.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Table S1 Cox regression maximum likelihood estimates for the effect of different covariates on the detection and depletion rates.

Figure S1 Overall mean seed survival under different seed dispersal scales (*D*), for *Messor arenarius* (white) and *M. ebeninus* (black).

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