

Directness and tempo of avian seed dispersal increases emergence of wild chiltepins in desert grasslands

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Summary

1. Seed dispersal is thought to be unpredictable and outside a plant's control. But directed seed dispersal by mutualistic birds can increase probabilities of germination and survival by the non-random deposition of seeds in suitable microhabitats.

2. In the Sonoran Desert grasslands of southern Arizona (USA), bird-dispersed wild chiltepin peppers (*Capsicum annuum* var. *glabriusculum*) grow in non-random association under bird-dispersed nurse trees and shrubs that serve as perches. We tested the hypothesis that the pattern is maintained by directional avian seed-dispersal patterns. Alternatively, post-dispersal processes, such as differential seed predation and seedling mortality, could create the associations.

3. For 3 years, we sampled the bird-generated seed rain under desert trees in four chiltepin subpopulations, comparing seed dispersal into microhabitats of fleshy-fruited trees and non-fleshy-fruited trees. *Celtis pallida* (fleshy-fruited) and *Prosopis vellutina* (non-fleshy-fruited) trees accounted for > 90% of the cover available for chiltepin recruitment. We tracked seedling emergence and survival in the two microhabitats and conducted a controlled seed-addition experiment to measure the effects of microhabitat, seed-addition density and temporal seed deposition on chiltepin emergence, growth and survival.

4. Approximately twice as many bird-dispersed seeds arrived at fleshy-fruited microhabitats compared with non-fleshy microhabitats. The numbers of seeds arriving and the number of seedlings emerging in microhabitats the following year were positively correlated. Survival of naturally emerged seedlings was similar at both microhabitats, but the seed-addition experiment revealed that more seeds are able to emerge under the denser foliage of fleshy-fruited microhabitats. The experiment also shows a significant effect of temporal deposition: when seeds were added gradually in a microhabitat (emulating repeated avian seed deposition under perches) instead of all at once, seedling emergence increased twofold on average.

5. **Synthesis:** Birds dispersed disproportionately high quantities of chiltepin seeds into favourable recruitment microhabitats, showing a case of directed dispersal. Birds also increase seedling emergence through the temporal deposition of seeds under fleshy-fruited trees, most likely as a result of reducing the odds of seed predation. A coupling between directed seed dispersal with classic facilitative plant–plant interactions leads to the formation of pattern and self-organization in a plant community.

Key-words: abiotic stress, dispersal in time, facilitation, frugivory, plant demography, plant neighbourhoods, plant–plant interactions, risk spreading

Introduction

The dispersal of seeds is unpredictable and outside a plant's control (Willson & Traveset 2000). Seed fate, however, can

be non-random and predictable depending where seeds arrive, germinate and recruit. Arid and heterogeneous environments where safe sites for recruitment are few and/or very patchily distributed can be more challenging than usual for seeds because those failing to arrive at suitable sites – usually microhabitats under nurse trees – will have almost no chance

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of surviving (Ehrlén & Eriksson 2000; Callaway *et al.* 2002). Under these conditions, processes that favour the dispersal of seeds into beneficial microhabitats will be especially advantageous (Levine & Murrell 2003). *Directed dispersal* by mutualistic seed-dispersing animals, such as birds, has been hypothesized to be such a process when they preferentially use favourable microhabitats to perch (Howe & Smallwood 1982; Wenny 2001). Still, only a handful of studies have measured its demographic consequences (Wenny & Levey 1998; García, Martínez & Obeso 2007; Briggs, Vander Wall & Jenkins 2009; Spiegel & Nathan 2011). Directed seed dispersal by frugivores could determine how plants move on heterogeneous landscapes and affect community assembly rules as frugivores disperse the seeds of the majority of plant species world-wide (Jordano 2000).

Directional dispersal becomes 'directed' dispersal when seeds arrive non-randomly in the most favourable microhabitats for plant recruitment (Howe & Smallwood 1982; Wenny 2001). The traditional alternative hypothesis is considered non-directed, or random dispersal, in which seeds reach microhabitats – whether suitable or not – in proportion to their availability. While many studies have examined the effects of environmental heterogeneity on the fate of seeds and seedlings (Ehrlén & Eriksson 2000), much less attention has been given to how dispersal, particularly frugivore-mediated dispersal, contributes to facilitative recruitment processes between plant species (García & Obeso 2003; García, Martínez & Obeso 2007).

Seed-dispersing animals can change the odds of seeds reaching different kinds of microhabitats (Schupp, Milleron & Russo 2002; Saracco, Collazo & Groom 2004; García, Zamora & Amico 2011; Carlo *et al.* 2013). For example, the movements and dispersal patterns of fruit-eating animals (a.k.a. frugivores) change according to the spatial distribution of fruiting resources (Levey 1988; Guitián & Munilla 2008; Côrtes & Uriarte 2012; Morales *et al.* 2012), habitat edges and corridors (Tewksbury *et al.* 2002; Levey *et al.* 2005), and forest gaps (Murray 1988). But frugivores not only disperse seeds to different locations, they also create a 'temporal' axis of seed deposition when they repeatedly deliver seeds to the same locations over time. The extent to which these behaviourally driven non-random seed-dispersal processes cascade through plant–plant interactions, population dynamics and plant community structure is little studied.

Here, we studied the directionality and demographic consequences of the bird-generated seed rain of the wild chiltepin pepper (*Capsicum annum* var. *glabrusculum*) in grasslands of the Sonoran Desert in southern Arizona. Previous work in the system has shown that chiltepins are associated non-randomly with nurse tree species that produce fleshy fruits that attract shared avian frugivores (Tewksbury *et al.* 1999; Tewksbury & Nabhan 2001). However, the mechanisms driving the pattern remain unclear. Our objective was to clarify the causes of the association. We hypothesized that chiltepins associate with avian-dispersed nurse shrubs because of directed seed dispersal. Alternatively, abiotic post-dispersal filters acting on the survival of seedlings could produce the same

association pattern, or both factors could be at work concurrently. For 3 years, we measured and compared the bird-generated seed rain of chiltepins under fleshy-fruited and non-fleshy-fruited nurse trees (hereafter non-fleshy) and examined patterns of both natural and experimental seedling emergence and survival under nurse tree types. Our results show that the pattern is maintained by directed seed dispersal and post-dispersal plant–plant facilitation operating in concert. The seed-addition experiment shows how avian dispersal can increase seed survival via the repeated seed deposition events into the same microhabitats.

Materials and methods

CHILTEPIN NATURAL HISTORY

Chiltepins – the wild ancestor of the dozens of cultivated varieties of hot peppers – are shrubs. The plants live for decades and reproduce exclusively via sexually produced seeds. Chiltepins living in the grasslands of the Sonoran Desert are found under the nursing shade of trees, shrubs or (less frequently) in the shade of large boulders or rocks. But almost never on the open ground that composes most of the terrain of the desert grassland (Tewksbury *et al.* 1999). Chiltepins experience rapid vegetative growth in the late summer through the early fall as a result of the late summer heavy monsoon rains. Blooming commonly starts 2–3 weeks after the first heavy downpours of July. The start of the monsoon also triggers the germination of seeds produced in the previous year. Although seed dormancy has been reported for the species and this particular variety (Randle & Honma 1981), our experience planting thousands of chiltepin seeds at the University of Washington glasshouses is that chiltepins from Tumacacori imbibe water easily and have nearly 100% germination rates 1 month after planting (Carlo, Tewksbury & Del Rio 2009). Fruits start ripening early in October and persist on bracts unless removed by birds through the fall and most of the winter months. A large chiltepin shrub can produce more than 5000 fruits in one season, with each fruit containing 10–35 seeds. Fruits are consumed by most of the passerine species present in Tumacacori, although thrashers (*Toxostoma* spp.) and northern mockingbirds (*Mimus polyglottus*) eat most of them and defecate seeds intact (Tewksbury *et al.* 2008).

STUDY SITE DESCRIPTION

The study was conducted on the slopes of Tumacacori Peak (31°33' N, 111°04'W) in the Wild Chilies Reserve, Coronado National Forest in southern Arizona. The site harbours the northernmost and largest population of wild chiltepins found in the United States (Tewksbury *et al.* 1999). The vegetation has a mixture of Sonoran Desert grassland and mesquite woodland without columnar cacti. Common fleshy-fruited trees and bushes found in Tumacacori are *Celtis pallida* (Cannabaceae), *Condalia* sp. (Rhamnaceae) and *Lycium andersonii* (Solanaceae). Common non-fleshy trees and shrubs are *Prosopis velutina* (Fabaceae), *Ziziphus obtusifolia* (Rhamnaceae), *Cercidium* sp. (Fabaceae) and *Fouquieria splendens* (Fouquieriaceae).

We worked on four subpopulations of chiltepins that we hereafter refer to as sites A (110 adult plants), B (40), C (51) and D (6). At all sites, chiltepins were found growing exclusively under trees and shrubs, where 66% were found in association with fleshy-fruited plants and the rest with non-fleshy plants (Fig. 1). We placed a metal tag in each plant and mapped them with GPS. For all adult plants, we

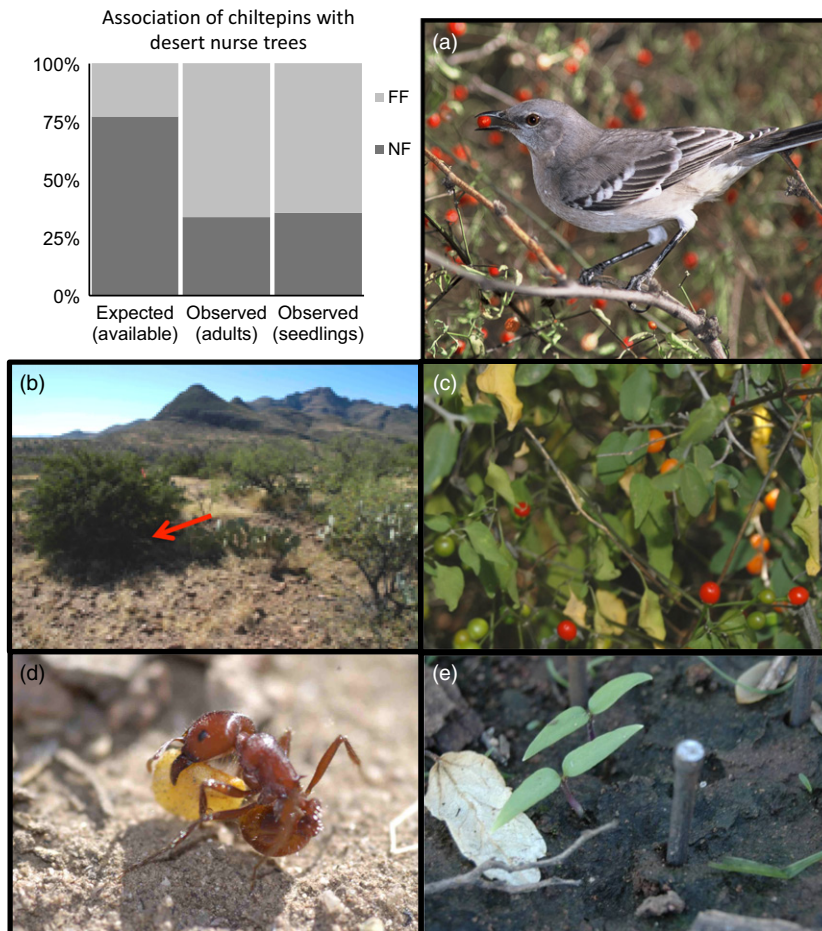


Fig. 1. Frequency of natural occurrence of wild chiltepins (*Capsicum annuum* var. *glabrusculum*) under shrubs and trees in Sonoran Desert grasslands in Tumacacori, southern Arizona. In this habitat, *Capsicum* only grows under the protective cover of shrubs and trees and is strongly positively associated with fleshy-fruited shrubs (FF) despite that non-fleshy-fruited plants (NF) provide the most abundant cover (207 plants, $\chi^2 = 160$, d.f. = 1, $P < 0.0001$). Panel a: Northern Mockingbird (*Mimus polyglottus*) feeding on chiltepins in Arizona. Panel b: view of study site, red arrow indicates location of a chiltepin plant. Panel c: detail of chiltepins (red and green fruits) present at the same time as the fruits of its *Celtis pallida* (FF) nurse tree (orange fruits in background). Panel d: harvester ant (*Pogonomyrmex* sp.) predated a chiltepin seed in the study site. Ant seed predation was commonly observed. Panel e: newly emerged chiltepin seedlings at an experimental seed-addition plot.

measured the cumulative cover (%) of tree and shrub species that shaded them. We also established 3 150×20 m plots to quantify the relative availability of tree cover (%), as well as the height, and canopy radius of shrub and tree species. The average proportion of vegetation cover from potential nurse trees and shrubs across sites was 23% fleshy-fruited plants (of which more than 90% were *Celtis pallida*) and 77% non-fleshy plants (of which more than 95% were *Prosopis vellutina*).

SEED RAIN OF CHILTEPINS UNDER DESERT SHRUBS AND TREES

In the fall and winter of 2005, 2006, and 2007, we used seed traps to sample the avian-generated seed rain of chiltepins under fleshy-fruited and non-fleshy nurse tree microhabitats. The traps were circular laundry baskets 44 cm in diameter (0.15 m^2) with a suspended net made from screen cloth (Carlo, Tewksbury & Del Rio 2009). Traps were covered with a steel mesh ($1 \times 1 \text{ cm}$) that kept vertebrates out (Appendix S1 in Supporting Information). Seed traps were never placed below or right next to adult chiltepins, thus the only way seeds could arrive on traps was via active dispersal by animals.

We sampled the seed rain from October through January. The content of traps was emptied twice each fall (Nov. & Jan.). In 2005, we placed 182 seed traps (site A: 36 fleshy-fruited and 40 non-fleshy; site B: 34 fleshy-fruited and 44 non-fleshy; site D: 28 fleshy-fruited and 18 non-fleshy). In 2006, we placed 265 traps (site A: 37 fleshy-fruited and 43 non-fleshy; site B: 30 fleshy-fruited and

34 non-fleshy; site C: 20 fleshy-fruited and 19 non-fleshy; site D: 40 fleshy-fruited and 40 non-fleshy). Last, in 2007, we placed 221 traps (site A: 34 fleshy-fruited and 35 non-fleshy; site B: 31 fleshy-fruited and 31 non-fleshy; site C: 27 fleshy-fruited and 25 non-fleshy; site D: 20 fleshy-fruited and 20 non-fleshy) (see Appendix S2 for placement maps). The placement of seed traps was almost the same across year for sites A, B and C, but site C was sampled only in 2006 and 2007. Other sampling differences among years are due to the loss of traps (e.g. damage by animals or wind) and that in 2006, twice as much effort was placed in sampling site D as part of a seed-dispersal study using ^{15}N stable isotopes (Carlo, Tewksbury & Del Rio 2009). To test for differences in the number of seeds arriving under fleshy-fruited and non-fleshy microhabitats for each year, we used zero-inflated negative binomial regression models (hereafter ZINB) in the SAS Proc CountReg platform (Version 9.2) (see Appendix S3 for further detail). The explanatory variables in the model were microhabitat (fleshy-fruited, non-fleshy), site (A, B, C, D) and a neighbourhood variable – the number of *Capsicum* plants within a 10-m radius from each trap. We used a 10-m radius to account for the influence of nearby chiltepins in the seed rain of traps because it was the distance at which chiltepin neighbourhoods were most influential in the seed rain collected in seed traps in 2 of 3 years (assessed by correlogram analysis, see Appendix S4 for more detail). We also used paired *t*-tests to examine differences in the cumulative number of seeds arriving at microhabitats across years (paired by year, and to test for differences in the yearly proportion of microhabitats reached by at least one chiltepin seed (paired by year).

NATURAL SEED RAIN, SEEDLING EMERGENCE, AND SURVIVAL

We conducted seedling censuses and followed the survival of up to 20 newly emerged seedlings per seed trap locations in 2005. This resulted in the tracking of 464 seedlings from August 2006 through January 2008 under 51 trees: 38 *Celtis* (fleshy-fruited microhabitat) nursing 260 seedlings and 13 *Prosopis* (non-fleshy microhabitat) nursing 204 seedlings. We examined the correlation between the number of seeds arriving in microhabitats and the number of emerged seedlings in the microhabitat. The survivorship of cohorts of chiltepin seedlings growing under fleshy-fruited and non-fleshy microhabitats was analysed with survival analysis (Kaplan–Meier with censored data, JMP version 7.0).

SEED-ADDITION EXPERIMENT

In the fall of 2006, we performed a seed-addition experiment to examine in controlled fashion, the relationship between seed arrival under trees and the emergence and survival of seedlings. We added a total of 33 600 chiltepin seeds, 16 800 seeds under *Celtis pallida* (fleshy-fruited) and 16 800 seeds under *Prosopis velutina* (non-fleshy). We established 16 plots in Tumacacori, located > 500 m away from the nearest chiltepin subpopulation but in the same type of habitat (Appendix S5). We used a randomized complete block design with three fully crossed experimental factors: 'microhabitat' (two levels: fleshy-fruited and non-fleshy), 'seed-addition density' (three levels: 10, 50, & 500 seeds) and 'seed-addition tempo' (two levels: all seeds added at once and seeds added in five different episodes with one-one-fifth of seeds added on each addition episode). In each plot, we also monitored microhabitats where no seeds were added to serve as negative controls. Seed-addition densities were modelled upon the values of the median, and 90th and 97.5th% quantiles (i.e. 10.5, 72.2 and 560.92, respectively) of the 2005 chiltepin seed rain (per trap). Seed-addition tempo levels were intended to account for the gradual natural seed deposition patterns produced by birds perching repeatedly at microhabitats over time.

Desert trees for the 12 seed-addition factor combinations were selected at random and tagged along each replicate transect. Only one factor combination was applied to a single tree. The location for seed addition was marked with a ground stake flag in the most densely shaded microhabitat underneath each tree (Appendix S5). All seeds for additions were harvested locally when fruit started to ripen in early October of 2006. Seeds in the 'all at once' addition-tempo treatment were added to plots during mid-October, while one-fifth of the seeds of the 'time dispensing' treatment were added once per week through late November. Seed-addition plots were monitored after each day of heavy rains during the early monsoon season in July through August 2007 and then rechecked in early September and mid-October 2007. To keep track of germination and deaths, we marked seedlings by placing a small steel nail at a distance of 2–3 cm. At every visit, we recorded the number of live and dead seedlings, and the height of the tallest seedling. All seedlings emerged during the first 3 weeks of August 2007. Seed-addition plots were checked again during the monsoon of 2008 to check for delayed emergence of dormant seeds. The proportion of emerged seedlings was analysed with a GLM (binomial error distribution) in JMP (version 7.0).

Results

A total of 11 248 chiltepin seeds were collected in our seed traps over the course of the three consecutive fall winters (see

Fig. 2 for average summaries). Of these seeds, 64.3% arrived in fleshy-fruited microhabitats (> 90% of which were *Celtis pallida*) and 35.7% under non-fleshy trees (> 95% of which were *Prosopis vellutina*), showing a significant directional pattern towards fleshy-fruited microhabitats (Fig. 2). All seeds were bird dispersed, and most were found still in bird droppings (droppings in the desert last months in almost intact form due to the lack of precipitation). On average, seed traps in fleshy-fruited microhabitats received twice as many seeds than seed traps in non-fleshy microhabitats (Fig. 2e). The yearly average proportion of seed traps receiving chiltepin seeds was also twice as high for fleshy than non-fleshy microhabitats (Fig. 2f). This is despite that fleshy-fruited microhabitats accounted for < 25% of the available microhabitat cover and non-fleshy microhabitats for > 75%.

Chiltepin seed arrival in microhabitats was not influenced by the height or the diameter of trees (correlations for 264 seed traps: height vs. seed count $r = 0.016$, $P = 0.80$; diameter vs. seed count $r = -0.013$, $P = 0.82$). But the density of

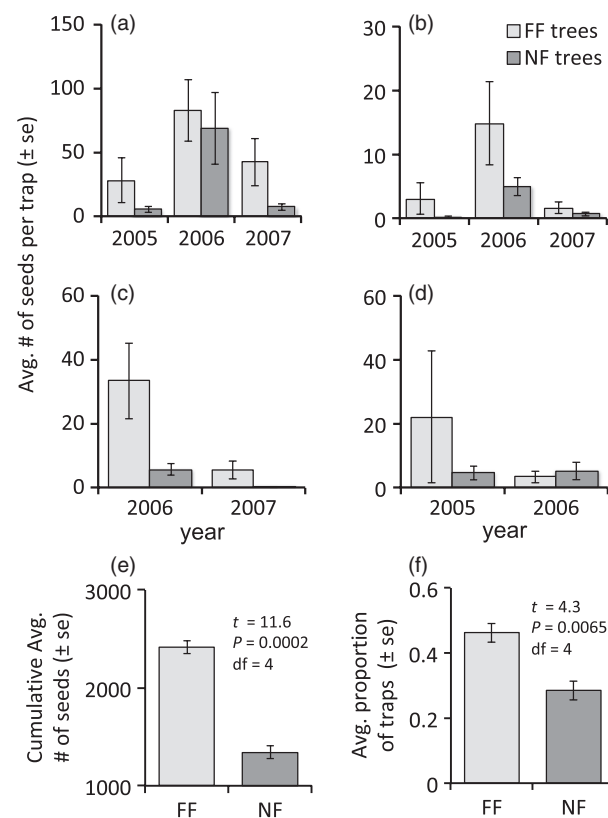


Fig. 2. Seed rain at fleshy-fruited microhabitats (FF, light grey) and non-fleshy microhabitats (NF, dark grey). Panels a–d: Yearly average seed rain on seed traps (0.15 m² trapping area) of wild chiltepins (*Capsicum annuum* var. *glabrusculum*) across sites a, b, c and d (respectively). In 2005, only sites a, b and d were sampled. All sites were sampled in 2006 and 2007, however, plants in site d during 2007 did not produced any fruit, and thus no seeds were found in seed traps of site d that year. Panel e shows the cumulative seed rain for 2005, 2006 and 2007 at each type of tree (analysis using data paired by year). Panel f shows the average yearly proportion of seed traps reached by at least one *Capsicum* seed under the two microhabitats (data paired by year).

adult chiltepins in the neighbourhood of microhabitats was positively correlated with seed arrival. The coefficients of the correlations between seed arrival and the density of adult chiltepins in the neighbourhood of microhabitats at increasing radii show significant correlation peaks at distances of 10–15 m from traps in all years of study (Appendix S4). Still, seed-rain differences between fleshy-fruited and non-fleshy microhabitats were not due to biases in the placement of seed traps, as there was no difference in the average density of chiltepins within a 10-m radius from seed traps under fleshy-fruited microhabitats as compared to traps under non-fleshy microhabitats in any sampling year (2005: $F_{1,179} = 2.05$ $P = 0.13$; 2006: $F_{1,261} = 0.51$ $P = 0.47$; 2007: $F_{1,179} = 1.46$ $P = 0.23$). The zero-inflated negative binomial (ZINB) regression models confirmed that non-fleshy microhabitats have negative effects on seed arrival in all years compared with fleshy-fruited microhabitats (Appendix S3). However, microhabitat effects on seed arrival for any particular study year show significant interactions with the 'site' variable. For example, Site A had the largest concentration of chiltepins, and for all years, this site shows a significant effect of microhabitat on seed rain in the statistical models, while sites with fewer plants showed non-significant differences in some years, thus producing a significant interaction between site and microhabitat (Appendix S3). The neighbourhood covariate (i.e. density of *Capsicum* plants within a 10 metre radius from a given seed trap) had significant positive effects on the number of seeds found at seed traps only for 2005 (for both NB & ZI model processes) and 2006 (ZI processes) and marginal importance and interactions in 2006 and 2007 (Appendix S3).

SEED RAIN AND THE EMERGENCE AND SURVIVAL OF SEEDLINGS IN FLESHY-FRUITED AND NON-FLESHY MICROHABITATS

In 2006, we found a total of 823 newly emerged chiltepin seedlings in sites A, B and D. Fleshy-fruited microhabitats contained 530 seedlings, and non-fleshy microhabitat had 293, showing that significantly more seedlings emerged from under fleshy-fruited than non-fleshy microhabitats ($\chi^2 = 252.9$, $P < 0.0001$). We found that the density of naturally emerged seedlings was low ($n = 34$ microhabitats, avg. seedlings = $9.36 \pm 4.75 \text{ m}^{-2}$ [mean \pm SE], median = 1.37; range 1–127 seedlings m^{-2}). When comparing the densities of naturally emerged seedlings between fleshy-fruited and non-fleshy microhabitats, we found no difference (pooled $t = 0.16$, d.f. = 32, $P = 0.87$). But the number of seedlings was positively related to the number of seeds arriving at the microhabitats in the previous year (GLM with Poisson errors: $\chi^2 = 272.7$, $P < 0.0001$). This relationship remains significant and positive for each microhabitat type separately (GLM for fleshy-fruited $\chi^2 = 264.9$, $P < 0.0001$; GLM for non-fleshy $\chi^2 = 53.5$, $P < 0.0001$). The survival of 464 of tagged seedlings (260 beneath fleshy-fruited and 204 beneath non-fleshy) did not differ between tree types (Kaplan–Meier survival analysis, $\chi^2 = 0.24$, $P = 0.624$). At the end of the

Table 1. Results of general linear model showing increased seedling emergence in fleshy-fruited microhabitats (*Celtis pallida*) than in non-fleshy microhabitats (*Prosopis pallida*) (see also Fig. 3). The proportion of emerging seedlings was modelled as a function of habitat (fleshy-fruited vs. non-fleshy microhabitat), experimental seed-addition density (10, 50 or 500 seeds) and seed-addition mode (added all at once or gradually) and interaction terms. Seeds were added in the fall of 2006, and emergence measured starting in the monsoon of 2007

Model effect	d.f.	χ^2	P
Microhabitat (Fleshy-fruited vs. Non-fleshy)	1	7.03	< 0.0080
Seed-addition density	2	0.71	0.6984
Seed-addition tempo	1	5.15	0.0232
Transect	14	7.10	< 0.0001
Microhabitat * Seed-addition mode	1	0.21	0.6435
Microhabitat * Seed-addition density	2	0.08	0.9602
Seed-addition density *	2	0.3219	0.8513
Seed-addition mode			

Whole Model Summary of Fit (likelihood ratio): $\chi^2 = 193.3$, $P < 0.0001$.

GLM details: Error distribution = binomial, Logit link function, Over-dispersion parameter = 3.85.

study in 2008, 3.8% of the seedlings were still alive in fleshy-fruited microhabitats, and 1.9% still alive in non-fleshy microhabitats.

SEED-ADDITION EXPERIMENT

A total of 708 seedlings emerged in 2007, 520 in fleshy-fruited microhabitats, representing an overall emergence rate of 1.5%, and 188 non-fleshy microhabitats, representing an overall emergence rate of 0.56%. These results show a strong effect of microhabitat type on seedling emergence (Table 1 and Fig. 3a). The way seeds were added also had a significant effect on seedling emergence (Table 1 and Fig. 3). The 'transect' factor (a blocking variable) explained much of the variation (deviance), showing large differences in germination between experimental localities. Curiously, no effect was detected for 'seed-addition density', or for any specified interaction term in the model. Irrespective of microhabitat and density of seeds added, gradual seed-additions treatments (mimicking avian seed dispersal) had about twice as many seedlings as those where seeds were added all at once (Fig. 3a). Seedlings were taller in fleshy-fruited than in non-fleshy microhabitats by October of 2007 (Fig. 3b, Appendix S5). Density of emerged seedlings did not negatively affect the growth of seedlings, but appeared positively correlated with it (Fig. 3c). However, by September of 2008, 100% of seedlings from experimental seed additions died in both microhabitat types irrespective of how they were added.

Discussion

Our results show that populations of wild chiltepins in desert grasslands are strongly limited by recruitment and heavily

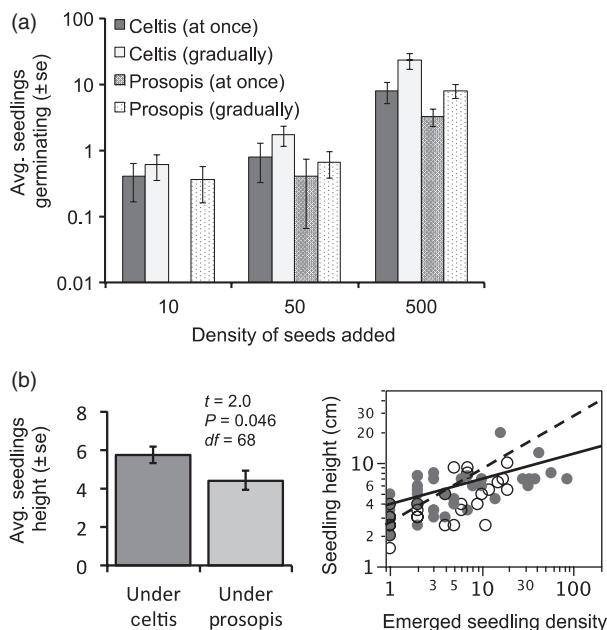


Fig. 3. Seedling emergence and height under *Celtis pallida* (fleshy-fruited) and *Prosopis vellutina* (non-fleshy), notice that y-axis is in logarithmic scale in (a). Seedling emergence in August of 2007 resulting from adding chiltepin seeds (*Capsicum annuum* var. *glabriusculum*) in October–November of 2006 in desert grasslands in Tumacacori, Arizona (Panel a). Significantly more seedlings emerged under *Celtis* than under *Prosopis* microhabitats (see Table 1 for statistical analysis). There was no significant effect of seed-addition density as proportions of emergence did not differ among treatments (Table 1). Compared with adding all seeds at the same time in microhabitats, adding seeds gradually significantly increased emergence the following year regardless of the microhabitat type (Panel a). Panel b: seedlings also grew taller in *Celtis* microhabitats than under *Prosopis* microhabitats (t -test on log-transformed seedling height: $t = -2.40$ d.f. = 68, $P = 0.019$). Panel c: the height of emerged seedlings was not negatively affected by crowding, but positively correlated with it. Solid line (for dark dots) shows correlation under *Celtis* ($r^2 = 33.6$, $F_{1,38} = 19.2$, $P < 0.001$), dashed line (for clear dots) shows correlation under *Prosopis* ($r^2 = 46.2$, $F_{1,28} = 24.0$, $P < 0.001$).

structured by avian dispersal among available microhabitats under nurse tree species. A combination of biotic and abiotic processes favours *Capsicum* recruitment under local fleshy-fruited trees as compared to non-fleshy-fruited trees: directional avian seed dispersal, environmental amelioration and increased seedling emergence. Of these three factors, directed seed dispersal appears to be the principal driver of the plant associations because seed arrival was positively correlated with seedling emergence in both types of microhabitats.

Despite comprising less than a fifth of the available nurse tree microhabitats, birds deposited more than twice the average number of seeds in fleshy-fruited than in non-fleshy microhabitats every year (Fig. 2e). The resulting natural patterns of seedling emergence reflected patterns of seed deposition in the microhabitats. For instance, 64.3% of all naturally emerging seedlings were found at fleshy-fruited microhabitats, while 35.7% were found at non-fleshy microhabitats. Curiously, the survival rates of these natural cohorts over the course of more

than 1 year appeared to be statistically indistinguishable. However, our controlled seed-addition experiment revealed higher emergence and early growth rates under fleshy-fruited shrubs, suggesting also that fewer seeds survive to germinate under non-fleshy shrubs (Fig. 3).

Harvester ants (*Pogonomyrmex* spp.) were very common in the study site and were observed preying chiltepin seeds in both the natural populations and experimental seed-addition plots (Fig. 1d). It is likely that the differences found in seedling emergence in the experiment were caused by more ant seed predation under the canopies of *Prosopis* than under *Celtis*. Grasses grow well under the scant canopy of *Prosopis*, but not at all under *Celtis*, and harvester ants forage preferentially on grassy habitats (Whitford 1978). Mammalian seed predators can be excluded from the picture as mammals are deterred by the capsaicins that make chiltepins very hot (Tewksbury & Nabhan 2001; Levey *et al.* 2006). Another alternative non-exclusive explanation for the reduced emergence of chiltepins under *Prosopis* is reduced by seed dormancy. The soil surface is hotter and dries faster under *Prosopis* (Tewksbury *et al.* 1999), which could make it more difficult for seeds to break dormancy and germinate. But the fact that chiltepins emerged only during the monsoon of 2007 (i.e. the year after the seed additions), and not one emerged during the following monsoon (2008), argues against dormancy as an explanation.

It must be underscored that the seed-addition experiment detected no effect of seed density on seedling emergence (Table 1). Birds and other frugivores commonly create foci of high seed densities under perching sites (Slocum 2001; Schupp, Milleron & Russo 2002; Russo & Augspurger 2004) where predation and/or competition can take a toll on recruitment and growth (Jordano & Herrera 1995; Spiegel & Nathan 2010, 2011). For example, Spiegel & Nathan (2010) showed that foci of high seed densities created by avian frugivores can negatively affect recruitment by creating 'death traps' and thus preventing directed dispersal from occurring. This does not appear to happen in this study system, as competition between chiltepin seedlings under fleshy-fruited nurse trees is minimal or non-existent. We observe very low numbers of seedlings per m² naturally emerging at the microhabitats (median = 1.37 seedlings per m² for sites containing at least one seedling), and there was no negative effect of seedling density on seedling survival or growth (Fig. 3c). Thus, seedling mortality due to abiotic stresses is clearly the main recruitment filter as chiltepins cannot grow in the open, and seedling mortality is very high even at 'safe' sites as evidenced by the little recruitment observed in the natural cohorts that we followed (i.e. $\leq 3.9\%$ survival following emergence). This contrasts with the desert plants studied by Spiegel & Nathan (2010), which can recruit in the open. Thus, for chiltepins, abiotic amelioration under fleshy-fruited trees appears more important as a facilitative mechanism than the potentially negative effects of intraspecific plant–plant competition in suitable microhabitats. As many of the seedlings we tracked died of water stress, it seems that the great yearly variability in rainfall is also an important determinant

of the fate of seedlings, and that very wet years are also necessary in addition to the thick nursing shade of *Celtis* shrubs.

EFFECTS OF SEED-ADDITION TEMPO ON SEEDLING EMERGENCE

The effect of seed-addition tempo on seedling emergence was significant and of similar magnitude to the effect size of microhabitat type on emergence (Table 1 and Fig. 3a). In fact, just by adding seeds gradually in five separate events, the number of emerging seedlings was doubled in every microhabitat, regardless of seed-addition densities (Fig. 3a). Because birds naturally deposit seeds under the same perching sites more gradually than we did, the effects of deposition tempo are likely to be stronger in nature than in our experiment.

Theoretically, seed deposition tempo should be expected to reduce risks of seed mortality by desiccation and/or by predation because mortality fluctuates along axes of both space and time (Ellner & Guckenheimer 2006). Thus, dividing a group of seeds into a higher number of discrete temporal packets, like birds and other vertebrate frugivores normally do, increases escape probabilities *in situ* in addition to *in space*, making it possible to spread predation risk over time. It is curious that all theoretical or empirical attention of endozoochory has been focused on spatial spread (Levin *et al.* 2003; and Ellner & Guckenheimer 2006; Clark *et al.* 2007), and no attention seems to have been given to this temporal aspect.

Chiltepin ripe fruits are consumed, and their seeds dispersed for periods lasting anywhere between two to four months. The duration of the fruiting period is determined by the size of the fruit crops of a particular year (i.e. the larger the crops the longer the dispersal season), which are ultimately controlled by the amount of rain. Thus, avian seed dispersal invariably results in gradual seed-addition events over 1–3 months. Tewksbury *et al.* (1999) showed using systematic field observations that the birds that disperse chiltepins in Tumacacori spend significantly more time perching and foraging in fleshy-fruited trees, especially inside the denser *C. pallida*. In *Celtis*, birds can hide more effectively from predators, find better shelter from abiotic stresses, and also feed on fleshy fruits (Tewksbury *et al.* 1999). This behaviour results in repeated movements among nurse tree locations and cause a temporal pattern of seed deposition. Effects related to the time of seed deposition should be more pronounced in wet years when the seed-dispersal season is longer due to the higher abundance of fruit.

Conclusions

The biases in the seed rain of chiltepins in Tumacacori can be properly called *directed* dispersal because non-random dispersal results in more seeds being deposited in microhabitats favourable to seedling emergence and growth. The finding that repeated seed deposition over time increases emergence *in situ* is important both theoretically and as a methodological consideration that ecologists should take into account when

performing seed-addition experiments. Our study also illustrates how the spatial templates formed by individual species' distributions in a plant community can structure the seed dispersal and recruitment patterns of frugivores. Similar directional feedbacks have been recently shown to operate at large spatial scales, where different types of tree patches and habitats dramatically increase probabilities of long-distance seed dispersal (LDD) (Carlo *et al.* 2013). Thus, frugivore-mediated feedbacks are an important mechanism by which organizational information, like the association of chiltepins with fleshy-fruited nurse shrubs, can propagate in space and time. Theoretical frameworks aimed at understanding self-organization in plant communities should not overlook the effects of pervasive directional seed-dispersal patterns created by mutualistic frugivores.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. View of seed trap design and typical desert nurse trees in Tumacacori, Arizona, USA.

Appendix S2. Maps showing the location of adult chiltepin plants and seed traps used to sample the seed rain.

Appendix S3. Tables showing parameter estimates and values of Zero Inflated Negative Binomial multiple regression models used to analyze the seed rain data.

Appendix S4. Correlogram showing the relationship between the number of adult chiltepin plants across different radii from the seed traps.

Appendix S5. Map showing the location of the 16 transects of the seed-addition experiment in Tumacacori, Arizona.