Empirical evaluation of directed dispersal and density-dependent effects across successive recruitment phases

Orr Spiegel* and Ran Nathan

Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Edmond J. Safra Campus, Jerusalem 91904, Israel

Summary

1. The directed-dispersal (DrD) hypothesis constitutes one of the main explanations for the adaptive value of seed dispersal in spatially heterogeneous environments. Traditionally, the DrD hypothesis asserts non-random arrival to specific sites where establishment conditions are independently favourable. Yet, enhanced arrival might negatively affect the establishment in otherwise favourable sites through enhanced density-dependent mortality (DDM). Since both density effects and habitat suitability might differ among establishment phases, assessment of habitat suitability should encompass the entire establishment process.

2. Here, we test the DrD hypothesis against a null model of random dispersal (RD) in an arid ecosystem where fleshy-fruited perennial *Ochradenus baccatus* shrubs are dispersed by two resident passerines. *Acacia* trees were predicted to present the favourable habitat in our system through the nurse-plant effect facilitating *O. baccatus* early establishment.

3. We determined expected seed arrival by monitoring the dispersers' time allocation among the different habitats and assessed habitat quality for different establishment phases: seed-phase survival (post-dispersal survival and germination) was determined by line transects, while early seedling survival was estimated by monitoring seedlings throughout the first dry season. Additionally, subsequent recruitment success was assessed by comparing the distribution of adult shrubs to that expected from the observed germination patterns.

4. When considering the expected seed arrival and early establishment (seed-phase and early seedling survival), the DrD hypothesis is supported: birds preferentially deposited seeds in habitats where conditions are favourable (e.g. under *Acacia* trees). Yet, considering recruitment success during later phases, the dispersal service provided by the birds was less beneficial than RD.

5. Effective density was indexed using the zone-of-influence approach in which densities are corrected by phase-specific sizes. We suggest that intense seed deposition into favourable habitats has led to strong DDM (presumably through competition) in those habitats during late establishment phases and was responsible, at least partially, for changes in habitat suitability across the recruitment phases.

6. *Synthesis.* Our results show that assessment of the DrD hypothesis depends on the context of the study (in terms of recruitment phases) since sites of enhanced seed arrival and high seed-to-seedling survival can ultimately prove unfavourable to the plant if density-dependent or other effects might increase mortality in these sites during later recruitment phases.

Key-words: density-dependent mortality, dispersal, disperser effectiveness, frugivory, *Ochradenus baccatus*, *Onychognathus tristramii*, *Pycnonotus xanthopygos*, safe sites, seed survival, zone of influence

Introduction

Seed dispersal is a key process shaping the spatial structure and the dynamics of plant populations and communities (Howe & Smallwood 1982; Nathan & Muller-Landau 2000).

*Correspondence author. E-mail: orr.spiegel@mail.huji.ac.il

The directed dispersal (abbreviated to DrD to avoid confusion with density dependence) hypothesis asserts that in spatially heterogeneous environments, dispersal bears a selective advantage if seeds preferentially arrive at sites that are particularly favourable for establishment (Howe & Smallwood 1982; Wenny 2001). Nearly all rigorous examples of DrD are cases of animal-mediated dispersal (Wenny 2001; Vander Wall & Longland 2004), presumably because, compared with abiotic dispersal vectors, animals tend to move to specific habitats in a predictable manner (e.g. Graham 2001; Wenny 2001; Aukema & del Rio 2002b; Leal, Wirth & Tabarelli 2007). For instance, bird-mediated seed dispersal in arid ecosystems is often highlighted as an illustrative case of DrD (Tewksbury *et al.* 1999; Wenny 2001; Green, Ward & Griffiths 2009). Woody species in these ecosystems often provide the only perches available for birds and thus induce highly non-random seed input when seeds are dispersed endozoochorily beneath perches. Furthermore, woody species in arid ecosystems often act as nurse-plants, facilitating seed survival and offering favourable establishment conditions since water and heat stress, rather than light availability, limit plant growth in these ecosystems (Valiente-Banuet & Ezcurra 1991; Fulbright, Kuti & Tipton 1995; Callaway *et al.* 1996; Tewksbury *et al.* 1999; Larrea-Alcazar & Soriano 2006).

Site suitability for establishment, however, might be uncoupled among recruitment phases. A habitat offering favourable conditions during early establishment might become unfavourable during later establishment stages (Schupp 1995; Buckley, Briese & Rees 2003; Schupp 2007). Moreover, as anticipated from the ideal free distribution hypothesis (Fretwell & Lucas 1969), suitability of a site depends not only on its quality but also on the number of individual consumers utilizing its resources (Spiegel & Nathan 2010). High seed deposition rate increases density and, consequently, can lead to higher mortality. Animal-mediated dispersal typically generates seed aggregations (Schupp, Milleron & Russo 2002; Kwit *et al.* 2007) that often develop into hotspots of high density-dependent mortality (DDM), possibly negating the advantage of favourable site characteristics (Schupp 1995; Kitamura *et al.* 2004; Russo & Augspurger 2004).

The importance of density-dependent processes in reducing seed-to-adult survival is widely acknowledged and might reflect several non-exclusive mechanisms such as seed predation, herbivory, pathogens and seedling competition (Janzen 1970; Donohue 1997; Nathan & Muller-Landau 2000; Mari *et al.* 2008). Mortality, reduced growth rate and other costs arising from high densities are often most pronounced during the late stages of the life cycle (Ramula & Buckley 2009) and might further decouple habitat quality across the recruitment process. For instance, competition for resources increases when seedlings start to utilize environmental resources from a growing zone of influence (ZOI) (Casper, Schenk & Jackson 2003; Berger *et al.* 2008; Ramula & Buckley 2009). Thus, using germination probability as a proxy for habitat quality might underestimate the density-dependent phase-specific costs if mortality is higher at later phases (e.g. during the seedling or the sapling establishment). It is therefore important to examine

the DrD hypothesis not only by tracing early recruitment phases (seed survival, germination and early seedling survival) but also by examining later phases when site suitability and recruitment success is ultimately determined (Nathan & Muller-Landau 2000; Wang & Smith 2002; Schupp 2007).

Recently, we have used an analytical model and simulations to examine how the trade-off between enhanced seed arrival and higher DDM affects the DrD in a simple environment composed of two (favourable and less favourable) habitats (Spiegel & Nathan 2010). These models examine how plant fitness depends on variation in the level of DrD (denoted as Ω in Spiegel & Nathan 2010), where DrD level is defined as the ratio between the number of seeds arriving at the favourable habitat under DrD and the expected seed arrival under a null model of random dispersal (RD). By solving the model for the two dispersal strategies and for two habitats, we found that the expected net fitness gain (ΔF) depends on various properties of the habitat and the plant and reaches a maximum (Ω^*) at intermediate DrD levels (Spiegel & Nathan 2010).

One of the key predictions of the model is that a dispersal vector concentrating seeds into a favourable habitat (hereafter simply a DrD vector) might reduce plant fitness because of enhanced DDM in this otherwise favourable habitat. Here, we test this prediction against field-collected data by extending this modelling approach to assess the adaptive value of DrD in relation to the RD in a landscape composing of several habitats, which may differ in seed arrival, density and suitability for establishment, and for several successive recruitment phases.

In this study, we assess how habitat suitability and disperser effectiveness (*sensu* Schupp 1993; Schupp, Jordano & Gomez 2010) change across establishment phases by testing the DrD hypothesis across different recruitment phases. A chronosequence approach (following a given cohort throughout the recruitment process) would have been ideal for this goal. However, such an approach is unfeasible for most perennial plants in general and for our study system in particular. Therefore, we compared the transition rates between different cohorts along the recruitment process. This approach relies on the assumption that the current situation in a given cohort in phase I represents the situation that preceded the current situation in phase II. For instance, that observed seed shadow is similar to the one that preceded the observed germinated seedlings. Additional assumptions of this approach are specified in the Materials and methods. Working in an arid ecosystem, where enhanced dispersal to specific sites inhabited by the so-called 'nurse-plants' has been considered a classic case of DrD (Wenny 2001; Godínez-Alvarez, Valiente-Banuet & Rojas-Martínez 2002), we quantified the seed shadow generated by two avian vectors dispersing a fleshy-fruited plant with respect to the presumed nurse-plants. We quantified habitat suitability for seed-phase survival, early seedling establishment and eventual recruitment of reproductive plants. Our results show that assessing habitat quality at different recruitment phases might lead to opposing conclusions: sites of enhanced seed arrival and seed-to-seedling survival can ultimately prove unfavourable to the plant if mortality in these sites is much higher at the seedling-to-adult transition, possibly because of DDM effects.

Materials and methods

STUDY SYSTEM AND SPECIES

The fieldwork was carried out in the lower part of Wadi Rahaf in the Judean Desert (near the Dead Sea), Israel (31′15°N, 35′22°E). The terrain is a rocky desert where the vast majority of plants are limited to isolated dry seasonal water courses (wadis). The wadi is confined between vertical cliffs. The common perennials are *Acacia raddiana* and *A. tortilis* trees, *Tamarix* spp. and *Capparis spinosa* shrubs. The most common large shrub at the site is *Ochradenus baccatus* Delile (Resedaceae), the focal species of this study. Adult *O. baccatus* shrubs are up to 2.5 m high and 6 m in diameter (H: 1.8 ± 0.1 m, D: 3.7 ± 0.3 m; mean ± SE; $n = 36$). They bear many fleshy berries that are consumed by a variety of passerines, mostly by the Yellow-vented bulbul (*Pycnonotus xanthopygos*) and Tristram's grackle (*Onychognathus tristramii*), the most abundant resident passerines of the region. Further details about the study site and an aerial photograph are provided in Appendix S1 in Supporting Information and in Spiegel & Nathan (2007).

HABITAT CLASSIFICATION AND COVER AREA

As neither the surrounding cliffs nor the 'matrix' area between adjacent wadis can be considered suitable for *O. baccatus* growth (i.e. shrubs are practically absent from the matrix), these areas were not included in this study. Within the wadi, we distinguished four habitat types that are hypothesized to differ in their suitability for germination and establishment of *O. baccatus*: (i) *Acacia* trees offer a shaded environment with sufficient understory room for shrub establishment. Additionally, the substrate is often less rocky under *Acacia* trees because tree roots reduce soil wash (Facelli & Brock 2000); (ii) Conspecific, mature *O. baccatus* shrubs were considered as an independent habitat for germinating seeds and young seedlings since they offer a shaded habitat but have low branches blocking understory

growth and might also have unknown negative effects such as allelopathy; (iii) *Tamarix* spp. and other shrubs also offer a shaded environment but unlike the *Acacia* trees, have low branches possibly blocking understory growth. Furthermore, the salt-shedding behaviour of *Tamarix* spp. through dropping salty leaf-litter possibly gives rise to high salinity soils (Ladenburger *et al.* 2006); (iv) Exposed habitat where intense direct solar radiation is expected to impair early establishment constitutes the major part of the area. The four habitats are named hereafter as 'Acacia', 'Ochradenus', 'Tamarix' and 'Exposed', respectively.

The relative area cover of the different habitats was calculated from a high resolution aerial photograph of the study site. Trees and shrubs were identified using GIS software (ArcMap 9.2 ESRI, Redlands, CA, USA). The results were also validated using line transects ($n = 10$, total length 1035 m) that were randomly selected and marked *in-situ* with iron pegs to allow repeated visits. Habitat cover was measured to the nearest decimetre using a standard measuring tape. These results coincided with our estimation of habitat area cover ($\chi^2_{d.f.=1} = 0.41$, $P = 0.52$), presented in Fig. 1.

HABITAT-DEPENDENT SEED DEPOSITION (SEED ARRIVAL)

To determine the proportion of seeds dispersed into the different habitats, we monitored the movement of bulbuls and grackles. Despite remarkable differences in their movement distances revealed by radiotelemetry, both species avoid the dry barren matrix between wadis, thus dispersing the vast majority of the seeds within the wadis' walls (see Appendix S1 for further explanation). Bird movement at the local scale (within the wadi) was observed from high vantage points on the wadi wall using a laser range finder (LaserAtlanta, Norcross, GA, USA) and binoculars. Birds were selected randomly and tracked in sessions that ended once visual contact was lost or if the focal bird could no longer be distinguished from other conspecifics.
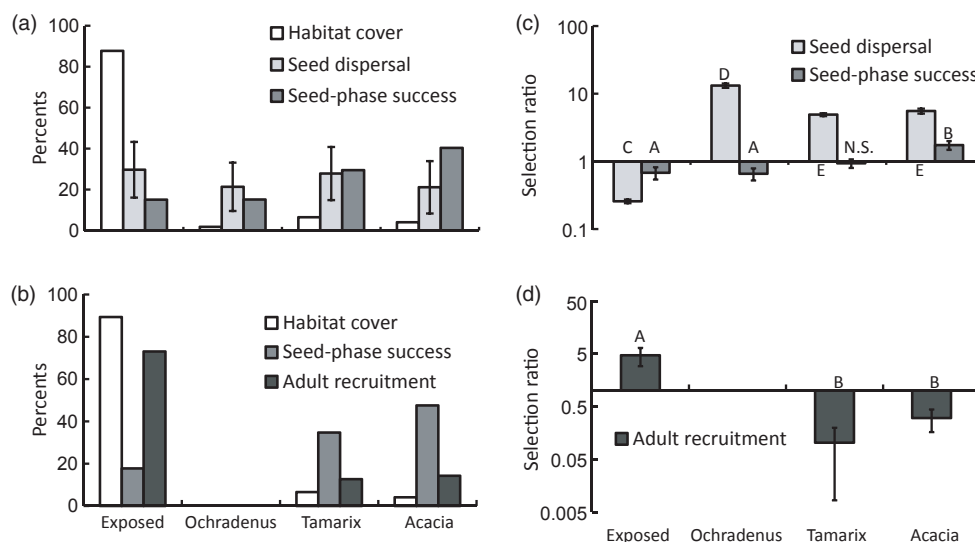

Fig. 1. Seed dispersal and establishment phases of *Ochradenus baccatus* in the different habitats. The left panels show proportional measures of the four habitats: (a) Habitat area compared with proportional deposition calculated from bird activity patterns (data from bulbuls and grackles combined according to their relative fruit consumption) and with the relative seed-phase success. (b) Proportional seed-phase success and habitat area compared with the proportional occurrence of adult *O. baccatus* shrubs. The right panels show the corresponding habitat-specific selection ratios. Ratios larger than one indicate positive enhancement. For instance, the selection ratio of 5.5 for seed dispersal into the 'Acacia' habitat in (c) indicates that birds occur in this habitat 5.5 times more than expected if they would have selected the habitat randomly according to their relative area. The 'Ochradenus' habitat is missing from the adult phase as classification of adult shrubs into this habitat is impossible. Error bars are ±95% confidence interval. Capital letters (right panels) indicate statistically different groups ($\alpha = 0.05$).

During the sessions, the birds' habitat and position was recorded every 15 s. The observations were performed once a week from December 2004 to May 2005, starting in the early morning until late afternoon, up to 60 h in total. Session durations were too short to include the effect of variation in seed gut retention time (GRT) on deposition pattern, and pseudo-replication is likely to occur since birds were not marked. Nevertheless, the small spatial scale of the study, where different habitats are within metres from each other (e.g. a bird can fly from an *Acacia* tree to a nearby shrub within a couple of seconds), implies a high transition rate among habitats and suggests our observations represent the overall time allocation between habitats and hence the bird-generated seed shadow within the wadi. Dispersal patterns, or simply the relative proportion of seeds arriving into each habitat, were calculated by combining data from both dispersal vectors according to their relative importance in *O. baccatus* fruit consumption (see Spiegel & Nathan 2007) using bootstrapping ($n = 2000$) to correct for differences in our sample size of vector locations.

In constructing bird-generated seed shadows, we assume that birds' movements reflect their seed deposition pattern and that there is no deposition-bias with respect to time allocation among habitats. We also assumed that the dispersal pattern created by these two main vectors reflects the total dispersal kernel (sensu Nathan *et al.* 2008) for this site. This assumption does not necessarily imply that the contribution of other dispersal vectors is negligible; rather, it necessitates that the contribution of other vectors to the seed shadow in each habitat is either similar to that generated by the study species (e.g. as for other bird species) or random (e.g. as for abiotic vectors). Non-dispersed seeds falling under their mother plant, secondary dispersal and post-dispersal seed predation may also play a role in redistribution of dispersed seeds. We further discuss this issue in the Discussion.

ESTIMATING HABITAT SUITABILITY

Since habitat suitability might differ across different phases of the plant life cycle, we estimated habitat quality separately for two non-overlapping recruitment phases: seed phase (post-dispersal seed survival and germination to a 5-cm seedling; this phase can be viewed also as germination *sensu lato*) and adult recruitment (seedling-to-adult). In addition to the two above-mentioned phases, we also examined the survival of young (5 cm) seedlings until the end of the first dry season, *c.* 6 months after germination. Although this provides an important insight into the process of phase-specific habitat suitability and DDM effects, it cannot be considered to be an independent phase as it is included in the initial part of the seedling-to-adult recruitment phase (i.e. survival from late seedling to adult cannot be determined). Therefore, we first describe the two non-overlapping phases (seed phase and adult recruitment) and then separately describe the additional analysis of seedling early survival.

Seed phase

Ideally, germination should be estimated experimentally through *in-situ* comparison of dispersed (or sown) seeds in the different habitats. Such an experiment could have helped distinguish seed differential survival from differential germination in each habitat. This approach, however, was not applicable for our study system since germination occurs during the winter (i.e. the rainy season, mostly between January and March), when flash-floods may impair successful deployment of experimental arrays by covering/relocating sown seeds, or simply by washing the arrays' markers without affecting the buried seeds. We therefore sampled naturally emerging seedlings and compared their proportions in the different habitats to the expected

proportions from seed arrival data. Since this approach actually couples seed deposition-to-germination survival and germination success, we hereafter refer to this phase as 'seed-phase survival'. Seedlings were sampled along the same transects described in the *habitat cover* section. All seedlings above the minimal size essential for identification (*c.* 5 cm, after emergence of the first non-cotyledon leaves) within three metres from both sides of the transect lines were counted and classified by habitat. To minimize errors, sampling was carried out simultaneously by two observers (holding a measuring tape to assure width limits were kept). We repeated the sampling three times throughout the germination season, *c.* 3 weeks apart.

Adult recruitment

While *O. baccatus* shrubs can produce fruits by the end of their second year, they reach their final size after many years (probably at the scale of tens of years). Consequently, a continuous monitoring approach of following specific individuals throughout the recruitment process is not applicable for quantifying habitat suitability during later recruitment phases. We therefore assessed the habitat suitability for later recruitment phases by comparing the distribution of adult (fruit bearing/flowering) *O. baccatus* shrubs to the distribution of seedlings among habitats (as sampled from the line transects). An underlying assumption here is that the observed seedling pattern and proportional habitat availability were similar to those that prevailed when the observed adult shrubs became established. Possible divergences from this assumption are discussed in the Discussion. All adult shrubs ($n = 196$) were surveyed, marked and classified to their habitats by GIS (based on their GPS locations). Since shrubs in the vicinity of a tree might benefit (or suffer) from its proximity, we applied a 10 m buffer around trees and other shrubs (i.e. an *O. baccatus* shrub < 10 m from a canopy polygon was considered as 'Acacia' or 'Tamarix' accordingly). Selection of buffer size is arbitrary and reflects our estimation of the area potentially influenced by *Acacia* and *Tamarix* trees through shading, salt-shedding and roots extending from the host tree canopy area. In addition, this buffer was selected to minimize inaccuracies arising from GPS position errors and aerial-photo geo-rectifying process. Adding such a buffer (applied for the adult shrubs only and not for seedlings that were sampled *in situ*) is conservative when comparing the proportion of adult *O. baccatus* in these two habitats with the higher proportions expected by the preceding establishment phase.

Early seedling survival

Habitat suitability for seedling establishment was quantified by monitoring seedling survival. Seedlings in all habitats were marked during the germination season of 2004 and monitored monthly along the dry season until November 2005. This period was selected because most of the seedling mortality in such arid ecosystems occurs during the first summer (dry season) (Maestre *et al.* 2003). To control for the effects of density, substrate quality and seedling age, seedlings were marked in cohorts of tens, each occupying an area of 1–2 m^2 (i.e. similar densities), and on as similar as possible substrates. All seedlings were roughly 5–7 cm tall when marked. Altogether 40, 40, 50 and 84 seedlings were marked in the 'Acacia', 'Ochradenus', 'Tamarix' and 'Exposed' habitats, respectively.

DATA ANALYSIS

To test whether the activity of the dispersal vectors (representing seed arrival) differs from the expected by RD (i.e. the relative proportions

of the four habitats), we used a modified version of the χ^2 goodness-of-fit test designated for habitat selection by animals (Manly *et al.* 2002, p. 50). This procedure takes into account also the variance in habitat use (between measurements, sessions in our case) and allows *post hoc* quantification of the selection/avoidance ratio for each habitat and the construction of confidence intervals for these selection ratios. A selection ratio > 1 for a given habitat at a given phase implies preferred transition probability for this phase in this habitat, whereas a value < 1 implies inferior transition probability. For instance, a selection ratio of two during the seed arrival phase to a certain habitat implies seed arrival is two times higher than expected from the habitat relative cover. Therefore, when comparing the observed seed arrival with the randomly expected arrival (according to the habitat cover), this parameter is similar in essence to the DrD level (Ω) in our model. When calculated for consecutive recruitment phases, the selection ratios allow phase-specific estimation of habitat suitability as described in the following paragraph.

Habitat suitability for the seed phase was determined by comparing the observed seedling emergence pattern (sampled in the line transect) with the pattern expected from the seed deposition pattern (from the vectors' combined time allocation). For determining habitat suitability for late establishment adults shrubs distribution was compared with the observed seedling emergence pattern. These comparisons were made using the same χ^2 statistics from Manly *et al.* (2002). The 'Ochradenus' classification is irrelevant to the seedling-to-adult recruitment phase as determining whether an adult shrub had originally germinated under a conspecific was not possible; thus, only three habitat classifications were used for this recruitment phase. We applied two adjustment methods, assuming that adult establishment in 'Ochradenus' habitat is either similar to adult establishment in the 'Exposed' habitat or zero. Both methods, however, yielded very similar results, and therefore only the latter approach, the more conservative one for examining DrD in this system (higher cost of enhanced dispersal into 'Ochradenus' habitat), is presented.

Estimation of early seedling survival was done by Cox proportional hazard regression using seedlings as the sample unit and the habitats as categorical predictors. The 'Exposed' habitat was set as the baseline. Cox regression allows comparison of the hazards in the different habitats, with higher values of the coefficient (Exp(B)) implying higher hazard and lower survival in relation to the baseline habitat. Seedlings that lost their tag or were still alive by the end of the surveillance (11%) were regarded as censored by last known date.

NET FITNESS GAIN OF THE DRD STRATEGY

To evaluate the potential contribution of the DrD vector to plants' fitness, we followed the same approach of Spiegel & Nathan's (2010) model: the expected *per-capita* net fitness gain of the DrD over the RD strategy (ΔF) was calculated by subtracting the expected fitness of the RD strategy (F_{RD}) from that of the DrD strategy (F_{DrD}) and summing over all habitats. This approach, using the habitat-specific and phase-specific selection ratios mentioned above, is further described in Appendix S1.

The average seed-phase survival ratio for all habitats is the ratio between overall seedling number and the overall seed production. Seed production is the product of (a) the number of adults in the relevant area, (b) the per-capita fruit production and (c) the average number of seeds per fruit. Seedlings quantities were estimated based on the availability in the area of the line transects; therefore, for consistency we use only adults within the same area (a = 85 plants). For fruit production, we used data from Wolfe & Shmida (1997) who worked at a nearby site (b = 83 fruits/plant). Seed quantities inside

a fruit were also measured previously (c = 11 seeds per fruit; Spiegel & Nathan 2007). Survival from seedling to adult was estimated from the average seedling-to-adult survival ratio (the ratio between seedling emergence and adult population) and habitat-specific selection ratio for this phase. Early seedling survival probability was estimated by the Exp(B) coefficients of the Cox regression (the odds hazard ratios). This provides the relative survival in the different habitats and the resulting number of seedlings with respect to the baseline at 0.5 survival probability.

Overall, although the actual number of survivors (e.g. seedlings, adults) changes with respect to our estimation of the average survival ratio for each phase, or with respect to the 0.5 cut-off point in the seedling establishment phase, the main scope of this analysis is to assess the net difference between the two strategies. This is standardized by the expected RD offspring number ($\frac{(F_{DrD} - F_{RD}) \times 100}{F_{RD}}$), making our evaluation of the net fitness gain insensitive to the average ratios.

DENSITY AND DDM ACROSS HABITATS AND PHASES

To explore how the effective density changes through the recruitment process, we calculated habitat-specific densities for three phases: arrival (seeds), post-germination (seedlings) and adults. For the latter two phases, the densities were calculated directly from the data, and for the arrival phase, densities were calculated by simply dividing the estimated seed production and estimated proportion of arriving seeds by the corresponding habitat area. As mentioned in the Data analysis section, the 'Ochradenus' habitat is not applicable for the adult phase.

The zone of influence (ZOI) approach was used for quantifying the potential increase in densities along the recruitment process. This is commonly viewed as an index of the strength of density-dependent intraspecific competition for resources (Weiner & Damgaard 2006; Berger *et al.* 2008), although alternative mechanisms of DDM may be also be involved. Multiplying the phase-specific density by the corresponding phase-specific ZOI allows quantifying the intensity of area usage at each phase for each habitat. The resulting dimensionless index can be viewed as index of effective density influencing various DDM mechanism including competition intensity. Higher values imply higher effective densities (e.g. facilitating stronger competition), with values larger than one (none in our scarcely covered study area) indicating overlap between individuals.

Although seeds do not compete until germination starts, once the radicle (the embryonic root; *c.* 1–3 mm in the case of *O. baccatus*) emerges, the seed begins absorbing water from its immediate surroundings. Thus, a radius of 5 mm was used for the 2-mm seed, representing their influence at the initial germination phase. A radius of 7 cm was used for the seedling phase, corresponding to maximal size of seedlings at the early establishment phase. A radius of 1.6 m was used for the adult phase corresponding to the mean plant radius.

Results

HABITAT-DEPENDENT SEED DEPOSITION (NON-RANDOM SEED ARRIVAL)

A total of 1153 and 2230 positions were observed for grackles and bulbuls (in 52 and 112 sessions), respectively. Session length distribution did not differ between species (05:26 ± 00:43 and 05:12 ± 0:27 min, Kolmogorov–Smirnov $Z = 0.662$, $P = 0.773$). Both species showed clear habitat preference, avoiding the 'Exposed' habitat (used for

19 ± 3% and 40 ± 7% of the time by bulbuls and grackles, respectively) and favouring the shaded habitats (18.6 ± 2.5% and 23.0 ± 5.6% in the 'Ochradenus', 37.4 ± 5.1% and 19.2 ± 8.5% in the 'Tamarix' and 26.4 ± 3.1% and 17.1 ± 5.6% in the 'Acacia' habitats by bulbuls and grackles, respectively). Despite major differences between species in flight distances (Spiegel & Nathan 2007), differences in time allocation among habitats were not significant ($\chi^2_{d.f.=3} = 3.8$, $P = 0.27$).

The combined activity pattern of the two bird species suggests seed deposition differs significantly from the RD null model for which the deposition pattern should reflect habitat cover ($\chi^2_{d.f.=3} = 154$, $P < 0.0001$, Fig. 1a). Post hoc comparisons of selection ratios for the different habitats suggest that time allocation in 'Ochradenus' was 13.1 times more than expected and stronger than selection for 'Tamarix' and 'Acacia' that were similarly selected for, with significant positive selection ratios of 4.9 and 5.5, respectively (Fig. 1c). Selection ratio for the 'Exposed' habitat was 0.25, suggesting a significant tendency to avoid this habitat. Note that the short visit duration to *O. baccatus* with respect to the birds GRT (see Spiegel & Nathan 2007) suggests that higher time allocation in the 'Ochradenus' habitat is likely to generate high seed influx into this habitat (defecation of seeds obtained on previous visits) and does not merely reflect long feeding events.

ESTIMATING HABITAT QUALITY

Seed phase

An average of 1349 (range 1169–1705) seedlings were sampled in three surveys of the line transects. Observed seed-phase pattern was significantly different from the one expected by dispersal ($\chi^2_{d.f.=3} = 114$, $P < 0.0001$, Fig. 1a), suggesting selective seed survival and\or germination success. In the 'Acacia' habitat, seed-phase survival was 1.7 times higher than expected while in the 'Exposed' and 'Ochradenus' habitats, seed-phase survival was significantly lower than expected with selection ratios of 0.65 and 0.67, respectively. In the 'Tamarix' habitat, seed-phase survival was not significantly different than expected by arrival (Fig. 1c).

Adult recruitment

The distribution of adult *O. baccatus* shrubs did not match the observed seedling distribution ($\chi^2_{d.f.=2} = 182$, $P < 0.0001$, Fig. 1b), but resembled the habitat cover. Although around 70% of the seedlings were found in the 'Acacia' and 'Tamarix' habitats combined, only a quarter of the adult shrubs were found in these two habitats (covering together roughly 12% of the area). Had adult recruitment been similar among habitats, a higher adult proportion should have been found in these two habitats. However, a negative selection during the late establishment phase prevails in these habitats (0.3 and 0.1, respectively; Fig. 1d), minimizing the proportion of adults in respect to seedling proportions. In contrast, the 'Exposed' habitat, where early establishment was mediocre, had a positive selec-

tion ratio of 4.6 for adult recruitment, favouring survival through late establishment. Although observed distribution of adult shrubs differs from the proportional habitat cover expected from the null RD model ($\chi^2_{d.f.=2} = 14.2$, $P < 0.0001$), none of the habitats differ in particular from the RD expectation (i.e. when adults are compared with habitat cover none of the selection ratios differ significantly from one). Put differently, the occurrence of 28 adult shrubs in the 'Acacia' habitat is somewhat higher than expected if dispersal was random (but not significantly higher as the confidence interval of the selection ratio of this scenario ranged from 0.5 to 8.1). On the other hand, this occurrence is far less than expected if seedling-to-adult survival were not considerably lower than in other habitats (and significantly so as the confidence interval for the selection ratio of this scenario ranges from 0.16 to 0.43).

Early seedling survival

The observed early seedling survival in our study site was very low, with the majority (89%) of the 213 seedlings we monitored dying during the first summer (a season characterized by dry and hot weather conditions) before the rainy season. Overall, seedling density in the study site was quite high (0.21 seedlings m^{-2}). Yet, early seedling survival differed among habitats even after controlling for differences in density among them (Table 1, Fig. 2). Seedlings growing in the 'Ochradenus' habitat had significantly higher chances of dying as compared with those in the 'Exposed' habitat, whereas in the 'Acacia' habitat seedlings experienced lower mortality compared with the 'Exposed' habitat baseline. Seedling survival in the 'Tamarix' habitat also showed similar trend of longer survival, but the difference from the 'Exposed' habitat was not significant (Table 1, Fig. 2).

NET FITNESS GAIN OF THE DRD STRATEGY

By considering differential arrival and suitability for seed-phase survival (germination) among habitats (i.e. habitat selection ratios for these phases, see Fig. 1), and summing up the expected number of offspring for all the habitats, we found

Table 1. Estimated hazard ratio coefficients (B and Exp(B)), standard errors (SE), Wald statistics and significance levels for the survival Cox regression model of seedlings, using 213 *O. baccatus* seedlings classified into four habitats using the 'Exposed' habitat as the regression baseline. High Exp(B) values indicate lower survival probability (in the 'Ochradenus' habitat), and lower values indicate better survival (in 'Acacia'). Significant values in the 'Ochradenus' and 'Acacia' habitats indicate that survival in these habitats differs from survival in the 'Exposed' habitat, yet survival in 'Tamarix' and 'Exposed' habitats is not statistically different

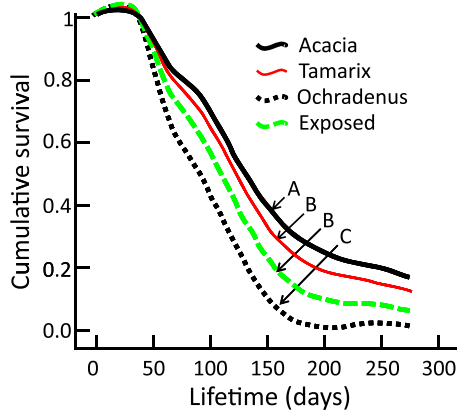| Habitat	B	SE	Exp(B)	Wald	d.f.	Sig.
Exposed				15.473	3	0.001
Acacia	−0.485	0.216	0.616	5.023	1	0.025
Tamarix	−0.256	0.197	0.774	1.690	1	0.194
Ochradenus	0.406	0.196	1.501	4.283	1	0.038

Fig. 2. Seedling survival functions during early seedling phase (the first dry season) in four different habitats. Capital letters indicate groups that are statistically significant from each other. Seedling survival in the 'Acacia' habitat is higher than in the 'Exposed' habitat used as a baseline, while survival in the 'Ochradenus' habitat is lower than this baseline. Survival in the 'Tamarix' habitat does not differ significantly from the baseline. Lines represent Spline interpolation of the functions, and letters represent statistically different functions using Cox regression ($\alpha = 0.05$).

that the DrD strategy yields more seedlings than RD and increases fitness (Table 2; first line). While the exact number of seedlings is sensitive to our estimation of the seed production because it determines our estimation of the mean seed-phase survival ratio (which is 0.01732 based on our calculations), the relative effect of the DrD strategy with respect to the RD strategy is not sensitive to this value because it depends only on the differential arrival and habitat selection ratios. In general, considering only suitability for seed-phase survival, the DrD strategy has a positive effect on fitness, yielding 39.3% more seedlings than the RD alternative.

By incorporating also differential survival at the early seedling establishment phase among habitats, the advantage of the DrD strategy is further reinforced because survival in the 'Acacia' and 'Tamarix' habitats is higher in comparison with the 'Exposed' habitat (expressed through the odds ratios from the Cox regression, 0.616 and 0.774, respectively; Table 1). The amplitude of the DrD advantage depends on the time after emergence cut-off point (dictating the proportion of surviving seedlings) and ranges between 39.3% and 61.7% more seedlings than the RD strategy. These values correspond to, respectively, cut-off periods allowing survival of *c.* 99% of the seedlings in the 'Exposed' habitat (i.e. average hazard ratio of 0.01) and a cut-off period allowing survival of *c.* 34% of the seedlings in this habitat (i.e. an average hazard ratio of 0.66). Although longer cut-off periods are empirically possible, the odd ratios estimated by the Cox regression approximation make such periods (i.e. higher hazard ratios) inapplicable because they give rise to unrealistic negative survival rate for the 'Ochradenus' habitat. At the median seedling survival level

Table 2. A comparison of the contrasting fitness contributions of the directed-dispersal (DrD) strategy and the random-dispersal (RD) null model across different recruitment phases. Rows represent the different recruitment phases shown in the transition map (DsS – dispersed seed, EmS – emerged seedling, M4S – a 4-month-old seedling and Adt – adult shrub). The 'mean transition probability' is the average over all habitats of EmS/DsS for phase 1 and of Adt/EmS for phases 2 and 4. For phase 3, transition probability is calculated for each habitat from the coefficient of the Cox proportional hazard regression (Exp(B); see text for details). 'Expected offspring' is the number of offspring summed for all habitats for each dispersal strategy. 'Net fitness gain' is the standardized effect of the DrD strategy with respect to the RD null model (i.e. $100 \times (\Sigma F_{DrD} - \Sigma F_{RD})/\Sigma F_{RD}$). When only habitat suitability for early establishment is considered (i.e. before density-dependent effects), DrD appears to positively affect fitness (*c.* 40–50% improvement). However, accounting also for the habitat suitability for later recruitment phases, the DrD strategy negatively affects plant fitness (*c.* −60% to −70%)

Transition map of the recruitment process	Phase	Mean transition probability	Expected offspring		Net fitness gain (%)	DrD effect
			RD (ΣF_{RD})	DrD (ΣF_{DrD})		
DsS → EmS (Phase: 1)	DsS → EmS (Phase: 1)	Phase 1: 0.017	964	1343	39.3	Positive
	DsS → EmS → M4S (Phases: 1 + 2)	Phase 1: 0.017 Phase 2:*	505	764	51.4	Positive
	DsS → EmS → Adt (Phases: 1 + 3)	Phase 1: 0.017 Phase 3: 0.011	36	11	−68.7	Negative
	DsS → EmS → M4S → Adt (Phases: 1 + 2 + 4)	Phase 1: 0.017 Phase 2:* Phase 4: 0.011	18	6	−60.1	Negative

*Calculated for 0.500 baseline survival ratio at $t = 125$ days. Survival ratio for other habitats: 0.250 for 'Ochradenus', 0.690 for 'Acacia' and 0.613 for 'Tamarix'.

in the 'Exposed' habitat (the regression baseline), the DrD vectors yield an improvement of *c.* 51% (Table 2; second line).

In contrast, considering both phases of the establishment process (seed-phase survival and seedling-to-adult survival), the relative effect of the DrD is negative, resulting in -68.7% offspring with respect to the RD (i.e. lower fitness). If differential early seedling survival is also included, the overall adult numbers decrease (one more mortality phase is inserted), but the net effect of the DrD compared with the RD strategy, although slightly weaker, is still very negative (-60.1%). As explained above, since the selection ratios of the seedling-to-adult phase do not specifically include the late seedling-to-adult survival probability, early seedling survival (where density is controlled) cannot be considered as an independent recruitment phase. Nevertheless, incorporating this phase is conservative when examining the DrD hypothesis as it further emphasizes the advantage of this strategy during early recruitment phases. Yet, even when early advantages are emphasized, the overall negative effects of the DrD strategy in our study system are prominent (Table 2; third and fourth line), suggesting that the RD strategy would yield higher fitness than DrD.

DENSITY AND DDM ACROSS HABITATS AND PHASES

Densities of *O. baccatus* decrease along successive recruitment phases (Fig. 3a) and are the highest in the 'Acacia' habitat. Differences in densities among habitats are consistent along the phases, except the adults being slightly denser in the 'Exposed' than in the 'Tamarix' habitats despite higher densities at the seedling phase in the latter habitat.

In general, the effective density (habitat use intensity) is rather low, reflecting the sparse nature of the vegetation in our ecosystem (Fig. 3b). Within habitat, effective density increases with successive recruitment phases, despite decreasing densities, suggesting that individuals' growing ZOI over-compensates for the decreasing densities. The effective density levels in the 'Acacia' habitat are higher than in any other habitat. Even in the seedling phase, the index is higher (0.0572) in this habitat than elsewhere for adults. In the adult phase, the index value (0.1505) is almost four times stronger than in the 'Exposed' habitat, suggesting more DDM (e.g. through more intense competition) are occurring in the former habitat.

Discussion

We estimated the fitness consequences of dispersal by combining tracking of vector movement – to assess their time budget among habitats and the associated dispersal pattern – with habitat suitability assessment across several successive phases of the recruitment process. We found that avian vectors (bulbuls and grackles) disperse *O. baccatus* seeds in a predictable manner, with high deposition rate in specific habitats (mostly under woody perches) and a clear tendency to avoid the exposed area. Based on habitat suitability for early recruitment, this dispersal pattern might have appeared beneficial for the plant and, consequently, has been interpreted as an example of DrD where seeds preferably arrive at favourable sites.
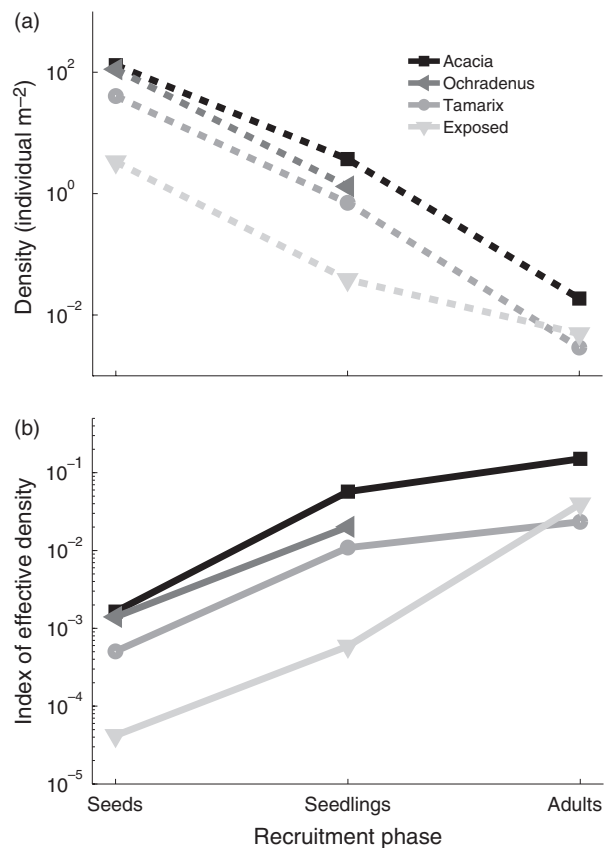

Fig. 3. Density and effective density along the recruitment process. (a) For all habitats, density declines from seeds to seedlings and from seedlings to adults. In the 'Acacia' habitat, densities are always higher than in the other habitats, and in the 'Exposed' densities are the lowest (excluding the adult phase where it is slightly higher than in the 'Tamarix'). (b) A dimensionless index of effective density or simply proportion of occupied area based on densities and zone of influence for each phase (often termed competition index). Index intensity increases with time and differs between habitats. In the 'Acacia' habitat, the index values are the highest, implying that adult shrubs in this habitat face effective density levels (and the associated density-dependent mortality risks) which are around fivefold stronger than in the 'Exposed' habitat, coming in the second place.

Yet, considering habitat suitability for the whole recruitment process clarifies that these 'DrD vectors' actually enhance seed arrival into less favourable habitats. Thus, in comparison with the null model of RD, avian vectors in our study system have negatively affected plant fitness. Evaluation of habitat suitability across several phases revealed these opposing trends by virtue of two (non-exclusive) processes. First, since habitat suitability might differ significantly among recruitment phases, a site favourable for germination (or for early survival) is not necessarily suitable for later survival and evaluation of habitat suitability across phases reveals this uncoupling in habitat suitability (Schupp 1995; Schupp 2007). Second, even if habitat suitability is constant across phases, high deposition rate in otherwise favourable sites negates their advantage by generating high density, intensifying competition and other density-dependent costs, as predicted by a recent revision of the DrD theoretical models (Spiegel & Nathan 2010).

THE IMPORTANCE OF ALTERNATIVE DISPERSAL
MECHANISMS

We assumed that the time budget of birds of two resident species reflects the overall seed shadow. This assumption might be impaired by several (non-exclusive) processes weakening the linkage between the actual seed shadow and observed vector movements. First, seedlings could have originated from non-dispersed seeds, biasing the seed shadow in a non-random manner by enhancing seed arrival into the 'Ochradenus' habitat. We have no information on the proportion of non-dispersed fruits or on the germination success of seeds from these fruits in field conditions. Nevertheless, our laboratory experiments revealed that germination success (*sensu stricto*) of seeds within intact fruits was considerably lower than the control groups of either pulp-removed or bird-digested fruits (38 ± 15%, 76 ± 2% and 66 ± 2%, respectively), weakening the potential contribution of this process to the effective seed shadow. Furthermore, even if such bias occurs, it is irrelevant to our interpretation of later phases and merely means that seed-phase survival in the 'Ochradenus' habitat is lower than estimated. Moreover, if this habitat is even less favourable than our estimation, the costs of strong bird-mediated dispersal into this habitat are even higher, reinforcing our conclusion regarding bird dispersal service being less effective than RD.

Second, primary or secondary dispersal by other vectors might also bias the results. The two focal species in this study are resident passerines that constitute, at least quantitatively, the most important biological vectors in the study site (Spiegel & Nathan 2007). Other bird species, mostly migratory passerines, presumably generate a similar seed shadow of enhanced arrival under woody perches within the wadi. Flash floods and possibly other dispersal vectors are likely to disperse fruits or bird-dispersed seeds in a random manner, blurring the strong spatial structure generated by the birds, for example, by transporting seeds from the 'Acacia' habitat to the 'Exposed' one. If this is the case, and flash-floods are an important vector randomly dispersing seeds, then the actual selection ratios for the seed phase are more extreme than our estimates: the seed-phase survival in the 'Acacia' habitat is actually higher since observed seedlings originated from fewer seeds. If so, this strengthens our conclusions that the birds *apparently* provide DrD when only the early recruitment phases are considered.

Third, other abiotic and biotic dispersal vectors and/or post-dispersal seed predators such as ants and rodents might operate and modify the bird-generated seed shadow (Vander Wall & Longland 2004). Again, such processes might alter our interpretation of the results only for the seed phase and not for later recruitment phases, and only if they re-distribute seeds among habitats in a non-random manner.

NON-RANDOM DISPERSAL AND ITS FITNESS
CONSEQUENCES

Contagious dispersal patterns characterize many ecosystems (Kwit *et al.* 2007). Examples of dispersal foci include conspe-cific or hetero-specific fruiting trees dispersed by frugivores (Clark *et al.* 2004; Kwit *et al.* 2007), ant nests and forest gaps (Wenny & Levey 1998; Leal, Wirth & Tabarelli 2007; Briggs, Wall & Jenkins 2009). The resulting seed aggregations often do not equally represent available habitats in heterogeneous environments. Our data clearly demonstrate a non-random arrival pattern where shaded habitats are over-represented in the seed shadow generated by the birds. Bulbuls and grackles spent 70% of their time on shrubs and trees used for foraging and perching, although these habitats covered only 12% of the study area. Green, Ward & Griffiths (2009), working in the same region on bulbul-generated DrD of mistletoe (*Plicosepalus acaciae*) seeds towards *Acacia* trees, reported a similar biased time allocation by the birds (66–93% of the time was spent on *Acacia* trees with 36 of the 40 observed defecations occurring in this habitat). The consequences of these non-random deposition patterns for plant fitness depend on the suitability of the deposition habitat for establishment. On the one hand, if seeds are deposited in a favourable habitat, DrD is achieved (Wenny 2001). On the other hand, non-random dispersal may be detrimental (in the case of a non-effective disperser) if deposition is directed towards an unsuitable habitat or if high densities lead to intense DDM (Kitamura *et al.* 2004; Russo & Augspurger 2004; Spiegel & Nathan 2010).

A clear distinction should be made between two qualitatively different possible scenarios relevant to the DrD hypothesis. First, the 'safe-site scenario' where the matrix is totally unsuitable and arrival at a safe-site is a prerequisite for establishment. Under these circumstances, usually relevant at a coarse spatial resolution, any enhanced arrival is a DrD. Examples include aquatic plants that must arrive at an ephemeral pool to establish or mistletoe seeds arriving at their host tree (Aukema & del Rio 2002b; Purves & Dushoff 2005). Similarly, as the area between adjacent wadis (i.e. the matrix) is inhospitable for *O. Baccatus*, arrival into the wadi (i.e. the 'safe-site') is an essential prerequisite for establishment. Birds clearly avoided this matrix and spent most of their time within wadis; therefore, in this sense, they do provide DrD to the favourable habitat.

Second, the 'habitat suitability scenario' is a more common situation of gradual difference in habitat suitability. In many cases, this is a finer spatial resolution version of the 'safe-site scenario' mentioned above, where suitable habitats are nested within a safe-site as defined above. Examples include specific branch diameters of the mistletoe host tree (Reid 1989) or a certain habitat within an ephemeral pool suitable for an aquatic plant. Our study system reflects a 'habitat suitability scenario', since habitats within the wadi differ in their suitability in a non-binary fashion. Estimation of habitat suitability is thus essential for proper interpretation of the disperser effectiveness and DrD (Schupp, Jordano & Gomez 2010). Since habitat suitability may change between different phases of the recruitment process (Buckley, Briese & Rees 2003; Schupp 2007), and because detrimental density effects may vary among recruitment phases (Ramula & Buckley 2009), habitat suitability assessment should encompass the entire establishment process.

DRD AND SITE SUITABILITY ACROSS RECRUITMENT PHASES

Phase-specific habitat suitability is a widely acknowledged phenomenon, with transition matrices calculated for different habitats and recruitment phases of many species (Buckley *et al.* 2005; Ramula & Buckley 2009; Caswell 2010). Yet, most of the empirical examples supporting the DrD hypothesis are based on short-term estimates of deposition site quality. Birds, rodents and ants are often considered DrD vectors (Wenny 2001; Vander Wall & Longland 2004; Giladi 2006); however, direct evaluations of habitat suitability through their relative contribution to offspring production are generally missing. In fact, many studies supporting the DrD were only based on one or more short-term proxies of habitat suitability, without testing the true suitability of the habitat (i.e. its potential contribution to plant reproduction). Commonly used proxies of habitat suitability are seed survival, germination ratio, seedling growth rate and early survival (Wenny & Levey 1998; Hollander & Vander Wall 2004; Leal, Wirth & Tabarelli 2007). However, our analysis demonstrates that the DrD-supporting conclusion of our study system could have been misleading if based on such short-term proxies (e.g. seed-phase and/or early seedling survival; Table 2), while longer-term assessment of habitat quality (although still a proxy of habitat true quality) revealed the disadvantageous effect of the dispersers in our study system.

Exceptionally, Briggs, Wall & Jenkins (2009) followed the fate of rodent-dispersed seedlings for 8 years and showed that chipmunks (*Tamias spp.*) provide directed dispersal of Jeffrey pine (*Pinus jeffreyi*) by caching seeds at the right depth and microsite. We are aware of only one other example where DrD was explicitly tested by considering habitat quality also for later phases of establishment: Pearson & Theimer (2004) showed that rodents provide DrD of Pinyon pine (*Pinus edulis*) by relating deposition site properties such as soil particle size and rock cover with their suitability for early establishment, together with distribution of adult trees among sites. Overall, we advocate complementing short-term estimation of the deposition-habitat quality with adult survey or fecundity estimation for this habitat when applicable.

SEED DEPOSITION AFFECTS SITE SUITABILITY THROUGH DENSITY EFFECTS

Bulbuls and grackles generated high seed aggregations under woody perches. For mistletoe dispersal studied by Green, Ward & Griffiths (2009), aggregations probably have only minor negative effects on establishment and might even confer positive effects if host resistance decreases with parasite load (Aukema & del Rio 2002a). Nevertheless, these aggregations might facilitate DDM of *O. baccatus* in our study site. While the patterns of enhanced seed-phase survival and early seedling survival in the 'Acacia' habitat support our initial prediction of nurse-plant effect by the *Acacia* trees, we argue that the low suitability of this habitat in the later phases is likely to result, at

least partially, from the high densities caused by the enhanced arrival to this habitat.

Obviously, in terms of individuals per metre, densities in all habitats were the highest at the seed phase and decreased with recruitment progression. Yet, accounting for the differences in biomass, or simply ZOI, effective density increased throughout the establishment (Fig. 3). Our observational methodology does not allow us to identify the process responsible for the DDM or assess their relative importance that may vary among recruitment phases. For instance, density-dependent predation might be important at the seed phase, while allelopathy might be more important at the early or late seedling phases, and competition more pronounced at late establishment phases. Although previous ZOI studies refer mostly to competition as the main mechanism responsible for DDM, other mechanisms might take place. Increasing index values suggest effective densities (and presumably competition levels) were the highest at the adult phase and agree with the general pattern of increasing density-dependent competition during the life cycle (Ramula & Buckley 2009). Moreover, Casper, Schenk & Jackson (2003) pointed out that when water and nutrients (in contrast to light) are limited, using aboveground size as a measure for ZOI might be an underestimation, since many arid-dwelling species have roots that are much larger than the canopy. It is very likely that the ZOI values used here for adult shrubs underestimate the actual values and that the resulting magnitude of competition during late recruitment phases is in fact higher than estimated. More generally, if plant response function to increasing density is not linear, then associated costs (whether the process responsible for the DDM is competition or other) might be even more severe at the 'Acacia' habitat where index values are the highest.

Effective density in the 'Acacia' habitat during the seedling phase was higher than in the adult phase in all the other habitats. In one instance, we counted more than 150 seedlings under a single medium-sized *Acacia* tree (not within the line transects). An average of 3.7 seedlings m^{-2} in the 'Acacia' habitat is clearly too high to allow late establishment and would have resulted in an improbably high (97%) degree of canopy overlap if all seedlings were to establish. Our finding of such high densities might appear inconsistent with the improved early seedling survival in this habitat. However, it should be noted that the early seedling survival estimation method controlled for density effects (by using similar densities for all 10-seedling cohorts across habitats), hence relaxing this disagreement. If DDM is indeed a limiting factor in this phase, using equal densities for comparing seedling survival across habitats might be biased because it selects for high-density hotspots and possibly underestimates the survival in other habitats where densities are generally lower (e.g. the 'Exposed'). Thus, the advantage of the 'Acacia' habitat might be even lower than calculated by our selection ratios, reinforcing our argument that the effectiveness of birds' dispersal service is low because of excessive-dispersal of seeds into this habitat.

Overall, regardless of the relative importance of DDM vs. density-independent changes of habitat suitability across the

recruitment phase, which is unknown, the avian vectors considered here generate high seed influx into habitats that appear to be less favourable to the plant. The low *O. baccatus* abundance in the 'Exposed' habitat may therefore reflect seed shortage rather than unfavourable conditions. In other words, our results support the main prediction from the theoretical model (Spiegel & Nathan 2010): avian vectors in our study system generated high DrD levels well above the intermediate optimal levels (Ω^*) that maximizes the net fitness gain (ΔF). DrD levels were too high, apparently yielding negative net fitness gain compared to the RD null model (Table 2). Similar patterns of contagious animal-mediated dispersal leading to high densities and clumped distribution patterns in later phases of the life cycle despite high DDM in those clumps were found also by Russo & Augspurger's (2004) study on the dispersal of *Virola calophylla* seeds by monkeys.

ALTERNATIVE EXPLANATIONS FOR THE ADAPTIVE VALUE OF BIRD-MEDIATED DISPERSAL

Fruit production is costly, especially in arid regions. Fruit characteristics that facilitate bird-mediated dispersal are selected if they are beneficial for the plant, implying that dispersal by avian vectors should yield some adaptive value (Lord 2004). Therefore, finding negative contribution of avian vectors to plant fitness in comparison with the RD strategy is puzzling. We suggest a few non-exclusive explanations to resolve the apparent contradiction. First, bird-mediated dispersal may bear alternative benefits for the plant. DrD is one of three main advantages postulated to promote seed dispersal. Two alternative benefits, conceptualized as the *Escape* and the *Colonization* hypotheses, suggest that any dispersal away from the mother plant is adaptive (Howe & Smallwood 1982). Possibly, bird contribution to these two aspects overcomes their negative effects through their deposition site selection.

Second, it can be argued that the DrD strategy should be compared to a null model other than RD, in particular with the local dispersal model where seeds fall mostly in the vicinity of the seed source or simply under the mother plant. In fact, although RD is a useful null model, a distance-independent random-dispersal kernel is unlikely, since most of the possible dispersal vectors actually generate a leptokurtic dispersal kernel (Clark *et al.* 2005). If birds are the alternative to having almost no dispersal at all, their contribution is beneficial despite the disadvantages illustrated in our study.

Third, as discussed above (in the 'safe-site scenario'), most of the region is actually inhospitable matrix between adjacent wadis. By enhanced seed dispersal into the wadis, birds do provide DrD to a safe site (the wadi). Any losses associated with the non-favourable habitat within the wadi are of minor importance to the hostile matrix avoidance. These aspects of dispersal, and the distance-related benefits at a larger spatial scale, were described previously (Spiegel & Nathan 2007).

Another limitation of this study may be related to the methodological approach of comparing cohorts rather than following a chronosequence approach. Specifically, this is most relevant to the determination of the habitat of adult *O. baccatus* shrubs. We have one anecdotal observation of a trunk belonging to a dead *Acacia* tree standing within a patch of a few well-developed *O. baccatus* shrubs in the 'Exposed' habitat. This observation raises the possibility that some of the adult shrubs currently found in the 'Exposed' habitat may have originated under *Acacia* trees that have subsequently died. The reverse switch, of shrubs germinating before the *Acacia* tree has established, is less likely since *Acacia* has a slow growth rate and most of the *Acacia* trees in our site are fully grown. More generally, if probabilities of habitat alternation during the life cycle of a shrub are biased towards some of the possible transitions, it might have noteworthy effects on our conclusions.

Finally, as with the constraints arising from the limited spatial scale of the study, the limited temporal scope of the research may also be misleading. Fruit characteristics are selected over a long temporal scale (evolutionary time-scale) and a wide range of conditions. Bird-mediated dispersal might be beneficial for other reasons (as stated above), or even from the DrD aspect if a large spatiotemporal scale is considered. As in any other fieldwork, the conclusion drawn here might represent a specific situation in time and space.

Conclusions

Our results suggest that bird-mediated dispersal, creating high seed deposition rates in habitats that are favourable for early recruitment phases, might eventually be detrimental for plant fitness when habitat quality is assessed for the entire recruitment process. We found that habitat quality is uncoupled across recruitment phases and that high deposition rates in the 'favourable' habitats, especially in the 'Acacia' habitat, might eventually lead to high densities during late recruitment phases and hamper habitat suitability. The costs of this enhanced deposition suggest that the over-abundance of *O. Baccatus* in these habitats reflects a biased deposition pattern rather than enhanced survival. The empirical results presented here support the main prediction of the revised DrD model (Spiegel & Nathan 2010) and emphasize that future improvements of the model should allow modelling of more than two habitats. Moreover, the influence of phase-specific habitat suitability should be added to the effect of density on habitat suitability for recruitment (which is already included in the model).

Empirically, reliable estimation of habitat suitability must be based on long-term evaluation of differential mortality across successive recruitment phases. In many ecosystems where the 'habitat suitability scenario' rather than the 'safe-site scenario' prevails, vectors that appear to provide DrD service on the short-term might prove to be less beneficial in the longer term. To the best of our knowledge, the present research is novel in relating DrD evaluation with habitat estimation over the entire recruitment process. Thus, we advocate long-term evaluation of habitat suitability in empirical tests of the DrD hypothesis. The conclusions of this research should be followed by experimental procedures that allow overcoming some of the methodological limitations discussed above, as well as determining the relative importance of DDM in deter-

mining phase-specific habitat suitability, and identifying the processes responsible for the DDM. Better understanding of DrD dynamics is essential for understanding mutualistic co-evolution of plants and animals and for effective management of ecosystems in which DrD is a key process.

Acknowledgements

References

Aukema, J.E. & del Rio, C.M. (2002a) Variation in mistletoe seed deposition: effects of intra- and interspecific host characteristics. *Ecography*, **25**, 139–144.

Aukema, J.E. & del Rio, C.M. (2002b) Where does a fruit-eating bird deposit mistletoe seeds? Seed deposition patterns and an experiment. *Ecology*, **83**, 3489–3496.

Berger, U., Piou, C., Schiffers, K. & Grimm, V. (2008) Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology Evolution and Systematics*, **9**, 121–135.

Briggs, J.S., Wall, S.B.V. & Jenkins, S.H. (2009) Forest rodents provide directed dispersal of Jeffrey pine seeds. *Ecology*, **90**, 675–687.

Buckley, Y.M., Briese, D.T. & Rees, M. (2003) Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. *Journal of Applied Ecology*, **40**, 481–493.

Buckley, Y.M., Brockerhoff, E., Langer, L., Ledgard, N., North, H. & Rees, M. (2005) Slowing down a pine invasion despite uncertainty in demography and dispersal. *Journal of Applied Ecology*, **42**, 1020–1030.

Callaway, R.M., DeLucia, E.H., Moore, D., Nowak, R. & Schlesinger, W.H. (1996) Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. *Ecology*, **77**, 2130–2141.

Casper, B.B., Schenk, H.J. & Jackson, R.B. (2003) Defining a plant's belowground zone of influence. *Ecology*, **84**, 2313–2321.

Caswell, H. (2010) Life table response experiment analysis of the stochastic growth rate. *Journal of Ecology*, **98**, 324–333.

Clark, C.J., Poulsen, J.R., Connor, E.F. & Parker, V.T. (2004) Fruiting trees as dispersal foci in a semi-deciduous tropical forest. *Oecologia*, **139**, 66–75.

Clark, C.J., Poulsen, J.R., Bolker, B.M., Connor, E.F. & Parker, V.T. (2005) Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology*, **86**, 2684–2694.

Donohue, K. (1997) Seed dispersal in *Cakile edentula* var. *lacustris*: decoupling the fitness effects of density and distance from the home site. *Oecologia*, **110**, 520–527.

Facelli, J.M. & Brock, D.J. (2000) Patch dynamics in arid lands: localized effects of *Acacia papyrocarpa* on soils and vegetation of open woodlands of south Australia. *Ecography*, **23**, 479–491.

Fretwell, S.D. & Lucas Jr, H.L. (1969) On territorial behavioral and other factors influencing habitat distribution in birds: I. Theoretical development. *Acta Biotheoretica*, **19**, 16–36.

Fulbright, T.E., Kuti, J.O. & Tipton, A.R. (1995) Effects of nurse-plant canopy temperatures on shrub seed gemination and seedling growth. *Acta Oecologica-International Journal of Ecology*, **16**, 621–632.

Giladi, I. (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos*, **112**, 481–492.

Godínez-Alvarez, H., Valiente-Banuet, A. & Rojas-Martínez, A. (2002) The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbaumia tetetzo*. *Ecology*, **83**, 2617–2629.

Graham, C.H. (2001) Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in southern Mexico. *Conservation Biology*, **15**, 1789–1798.

Green, A.K., Ward, D. & Griffiths, M.E. (2009) Directed dispersal of mistletoe (*Plicosepalus acaciae*) by Yellow-vented Bulbuls (*Pycnonotus xanthopygos*). *Journal of Ornithology*, **150**, 167–173.

Hollander, J.L. & Vander Wall, S.B. (2004) Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). *Oecologia*, **138**, 57–65.

Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.

Kitamura, S., Yumoto, T., Poonswad, P., Noma, N., Chuailua, P., Plongmai, K., Maruhashi, T. & Suckasam, C. (2004) Pattern and impact of hornbill seed dispersal at nest trees in a moist evergreen forest in Thailand. *Journal of Tropical Ecology*, **20**, 545–553.

Kwit, C., Levey, D.J., Turner, S.A., Clark, C.J. & Poulsen, J.R. (2007) Out of one shadow and into another: causes and consequences of spatially contagious seed dispersal by frugivores. *Seed Dispersal: Theory and its Application in a Changing World* (eds A.J. Dennis, E.W. Schupp, R.J. Green & D.W. Westcott), pp. 427–444. CAB International, Wallingford, UK.

Ladenburger, C.G., Hild, A.L., Kazmer, D.J. & Munn, L.C. (2006) Soil salinity patterns in Tamarix invasions in the Bighorn Basin, Wyoming, USA. *Journal of Arid Environments*, **65**, 111–128.

Larrea-Alcazar, D.M. & Soriano, P.J. (2006) Spatial associations, size-distance relationships and population structure of two dominant life forms in a semiarid enclave of the Venezuelan Andes. *Plant Ecology*, **186**, 137–149.

Leal, I.R., Wirth, R. & Tabarelli, M. (2007) Seed dispersal by ants in the semiarid caatinga of north-east Brazil. *Annals of Botany*, **99**, 885–894.

Lord, J.M. (2004) Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecology*, **29**, 430–436.

Maestre, F.T., Cortina, J., Bautista, S., Bellot, J. & Vallejo, R. (2003) Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. *Ecosystems*, **6**, 630–643.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L. & Erickson, W.P. (2002) *Resource Selection by Animals: Statistical Design and Analysis for Field Studies*. Kluwer Academic Publishers, Dordrecht.

Mari, L., Casagrandi, R., Gatto, M., Avgar, T. & Nathan, R. (2008) Movement strategies of seed predators as determinants of plant recruitment patterns. *American Naturalist*, **172**, 694–711.

Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278–285.

Nathan, R., Schurr, F.M., Spiegel, O., Steinitz, O., Trakhtenbrot, A. & Tsoar, A. (2008) Mechanisms of long-distance seed dispersal. *Trends in Ecology & Evolution*, **23**, 638–647.

Pearson, K.M. & Theimer, T.C. (2004) Seed-caching responses to substrate and rock cover by two *Peromyscus* species: implications for pinyon pine establishment. *Oecologia*, **141**, 76–83.

Purves, D.W. & Dushoff, J. (2005) Directed seed dispersal and metapopulation response to habitat loss and disturbance: application to *Eichhornia paniculata*. *Journal of Ecology*, **93**, 658–669.

Ramula, S. & Buckley, Y.M. (2009) Multiple life stages with multiple replicated density levels are required to estimate density dependence for plants. *Oikos*, **118**, 1164–1173.

Reid, N. (1989) Dispersal of mistletoes by honeyeaters and flowerpeckers: components of seed dispersal quality. *Ecology*, **70**, 137–145.

Russo, S.E. & Augspurger, C.K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, **7**, 1058–1067.

Schupp, E.W. (1993) Quantity, quality and effectiveness of seed dispersal by animals. *Vegetatio*, **107/108**, 15–29.

Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409.

Schupp, E.W. (2007) The suitability of a site for seed dispersal is context-dependent. *Seed Dispersal: Theory and its Application in a Changing World* (eds A.J. Dennis, E.W. Schupp, R.J. Green & D.W. Westcott), pp. 445–462. CAB International, Wallingford, UK.

Schupp, E.W., Jordano, P. & Gomez, J.M. (2010) Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, **188**, 333–353.

Schupp, E.W., Milleron, T. & Russo, S.E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed Dispersal*

and Frugivory: Ecology, Evolution and Conservation (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 19–33. CABI International, Oxfordshire, UK.

Spiegel, O. & Nathan, R. (2007) Incorporating dispersal distance into the disperser effectiveness framework: frugivorous birds provide complementary dispersal to plants in a patchy environment. *Ecology Letters*, **10**, 718–728.

Spiegel, O. & Nathan, R. (2010) Incorporating density dependence into the directed-dispersal hypothesis. *Ecology*, **91**, 1538–1548.

Tewksbury, J.J., Nabhan, G.P., Norman, D., Suzan, H., Tuxill, J. & Donovan, J. (1999) In situ conservation of wild chiles and their biotic associates. *Conservation Biology*, **13**, 98–107.

Valiente-Banuet, A. & Ezcurra, E. (1991) Shade as a cause of the association between the Cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacan valley, Mexico. *Journal of Ecology*, **79**, 961–971.

Vander Wall, S.B. & Longland, W.S. (2004) Diplochory: are two seed dispersers better than one? *Trends in Ecology & Evolution*, **19**, 155–161.

Wang, B.C. & Smith, T.B. (2002) Closing the seed dispersal loop. *Trends in Ecology & Evolution*, **17**, 379–385.

Weiner, J. & Damgaard, C. (2006) Size-asymmetric competition and size-asymmetric growth in a spatially explicit zone-of-influence model of plant competition. *Ecological Research*, **21**, 707–712.

Wenny, D.G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, **3**, 51–74.

Wenny, D.G. & Levey, D.J. (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 6204–6207.

Wolfe, L.M. & Shmida, A. (1997) The ecology of sex expression in a gynodioecious Israeli desert shrub (*Ochradenus baccatus*). *Ecology*, **78**, 101–110.

Supporting Information

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

Appendix S1. Complementary methodological details.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.