Frugivore behaviour determines plant distribution: a spatially-explicit analysis of a plant-disperser interaction

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The spatial distribution of plants (and other primarily sessile organisms) depends on the interplay between their ecological requirements and the spatial template set before, during, and after the dispersal process. In the case of animal-dispersed plants, the spatial characteristics of animal behaviour during the seed dispersal process are likely to leave a lasting imprint on plant distribution. Here, we hypothesize that the activity patterns of the frugivorous lizard *Podarcis lilfordi* directly influence the spatial distribution of the fleshy-fruited shrub *Daphne rodriguezii*. To evaluate this hypothesis, we first analysed lizard activity, following radio-tracked lizards during the plant's fruiting period, and identified its main determinants at several spatial scales of habitat aggregation (from 12.5 to 150 m). We hypothesised that lizard activity depends on differential habitat features explaining its territory use plus habitat preferences associated with each movement bout. In a second step, the most important determinants of lizard activity plus the variables describing habitat structure were used to predict the presence of adult and juvenile plants. Predictability of lizard activity (based on AUC and Pearson regression coefficients) was higher at broad spatial-scales of habitat aggregation (75 m). The two best predictors of lizard activity were the habitat features of and the distance to the core area (defined as the area enclosing the 0.50 cumulative probability of lizard locations). Plant presence was best predicted by models based on a combination of lizard activity and habitat features at local spatial scales (1.5 m). Best models included habitat features and lizard activity for adult plants, and local-scale habitat features, the proximity of adult plants and lizard activity for juveniles. In both cases, most plants (50–60%) were located at 'optimal sites' (both favourable for lizards and with adequate habitat features), whereas a small fraction of them (3–10%) were located at dispersal-limited sites (i.e. with adequate habitat features but suboptimal for lizards). Our results thus suggest that the interplay between lizard activity and local habitat features determines the spatial patterns of juvenile-plant presence and leaves a lasting signature on adult-plant distribution.

Understanding the distribution and abundance of organisms in space, relating them to attributes of the landscape they inhabit, and detecting the spatial scales at which such attributes operate represent central questions in modern ecology (Turner et al. 2001). Landscapes represent spatially-heterogeneous areas in which organisms select their resources and are influenced by the operation of various ecological processes (Turner et al. 2001). Species often differ in the scale at which they perceive and exploit the different landscape elements (Solon 2005); hence, the same landscape may exhibit completely different structures when viewed with the eyes of different organisms (Wiegand et al. 1999).

In mobile organisms, especially animals, resource selection often takes place at various, nested spatial scales (Johnson 1980, Manly et al. 2002, Mayor et al. 2009). The largest scale is the geographic range of a species, which encompasses populations or meta-populations. Within populations, individual home-ranges (or territories) are selected; within-territories, other general features such as habitat types may be selected; and within habitat types, finer-scale elements (e.g. food items, shelter) may become important (Manly et al. 2002).

In contrast, organisms that are sessile in most of their life-stages, such as plants, depend more strongly on the patterns of resources in their immediate vicinity (Law et al. 2001); however, their distributional patterns may be also influenced by larger-scale factors that determine their dispersal and establishment. One the one hand, plants are more sensitive to fine-scale environmental factors (e.g. humidity, habitat, radiation); on the other hand, they often depend on the patterns of displacement and resource preference of organisms that interact with them (e.g. animals that feed on them, pollinate their flowers or disperse their seeds).

In the case of animal-dispersed plants, understanding their distribution and abundance may require studying both the suitability of local habitats for the plants and their use and/or preference by the seed disperser (Schupp and Fuentes 1995). A key element is, thus, how animal habitat preferences (i.e. the likelihood of an animal selecting a given item when offered alternative choices on an equal basis; Beyer et al. 2010 and references therein) influence the spatial patterns of plants – therefore determining its interaction with local habitat structure. Seed dispersal is a critical process that links

the movement of frugivores with the distribution of plants (Russo et al. 2006, Santamaría et al. 2007, Culot et al. 2010). Plants move when they are dispersed and, thus, the spatial effect of a potential habitat on them can only emerge after the seed dispersal process. In general, seed dispersal mediated by animals creates non-random seed shadows (Cousens et al. 2008) due to the response of frugivores to landscape configuration (habitat, plant species and topographic features) and/or to behavioural processes (Wenny 2001, Russo and Augspurger 2004, Westcott et al. 2005, Russo et al. 2006). Because plant survival often is extremely heterogeneous and dependent on fine-scale environmental conditions, any aspect of frugivore behaviour that results in seed deposition towards favourable environments may increase plant fitness (Wenny 2001, Kwit et al. 2004). There are also cases, however, in which plants are found predominantly at suboptimal habitats because frugivore preferences favour seed deposition in such sites (Fragoso 1997).

Narrowly-specialized, one-on-one plant-disperser interactions are rare in nature, and they offer important cases that allow us to study, in isolation, how and to what extent individual frugivore species influence the distribution and population dynamics of their plant partners (Babweteera et al. 2007, García et al. 2009). Hence, the mutualistic interaction between the fleshy-fruited shrub *Daphne rodriguezii* (Thymelaeaceae) and the frugivorous lizard *Podarcis lilfordi* (Lacertidae) in a western Mediterranean island represents an excellent dispersal system in which to evaluate whether habitat-dependent frugivore preferences cascade into the spatial pattern of the dispersed plant. *Podarcis lilfordi* is the exclusive, single disperser of *D. rodriguezii* and its presence has been shown to be essential for the regeneration of this plant species (Traveset and Riera 2005).

In this study we analyze data on the habitat preference and movement of the lizard *P. lilfordi*, as well as the presence of juvenile and adult individuals of the shrub *D. rodriguezii*, to: a) identify the major determinants and critical scales of lizard activity, measured in terms of territory use and movement between habitat patches; and b) explore whether the movements and habitat preferences of the disperser leave a signature in the spatial pattern of plant distribution, and whether such pattern is modified by the habitat features of the seed-deposition sites. To this end, we proceed in three steps: 1) we predict lizard territory use at three scales (home-range, core-area and patch preference) by fitting lizard-relocation data to sets of habitat variables using scale-dependent generalized linear models; 2) we predict lizard displacement distances (step distance, distances from the centroid of the home-range and core area) based on the habitat features of the start and end site; and 3) we predict the presence/absence of juvenile and adult plants based on the observed distribution of habitat features and the predictions of models describing lizard activity (fitted in the two previous steps). Using these results, 4) we evaluate the relative contributions of seed dispersal by lizards and local habitat features in determining plant distribution patterns, and whether such contributions change along the plant's life cycle (from juveniles to adults).

Material and methods

Study system

Podarcis lilfordi is a small diurnal lizard endemic of the Western Balearic Islands (Mallorca and Menorca, W Mediterranean), which plays an important role in the reproductive potential of many native plants (Traveset and Sáez 1997, Traveset and Riera 2005). It behaves as a central-place forager, searching for food around its territory and returning to its central point in less than four days (Santamaría et al. 2007).

Daphne rodriguezii is a small evergreen shrub, endemic to the coastal shrubland of Menorca Island. Their fruits (orange-red drupes) develop in May–June and are quickly consumed by *P. lilfordi* lizards if these are present. After consumption, *D. rodriguezii* seeds pass quickly (one to six days) through the lizard's gut and are dispersed along its movement track (Santamaría et al. 2007). There is only one population left where the interaction between *D. rodriguezii* and *P. lilfordi* can still be studied (Colom Islet) since, in all other populations of *D. rodriguezii*, the lizard is already extinct. Direct observations and exclusion experiments showed that other frugivores do not consume *D. rodriguezii* fruits, and the plant therefore fails to recruit at sites where the lizard is absent (Rodríguez-Pérez and Traveset 2010).

Study site

Field work took place at the Colom Islet, a small islet (ca 60 ha) located ca 200 m offshore of Menorca Island (Supplementary material Fig. A1). The study site was located in a small peninsula (2.91 ha) situated at the south-western tip of the islet (Supplementary material Fig. A1), covered by sclerophyllous garrigue dominated by 'broad-leaf shrubs' (1–2 m height, including broad-leaf, fleshy-fruited species such as *Phillyrea latifolia* and *Pistacia lentiscus*) and 'narrow-leaf shrubs' (0–1 m height, including narrow-leaf, dry-fruited species such as *Erica multifolia*, *Rosmarinus officinalis* and *Santolina chamaecyparisus*). A large part of the study site was covered by bare soil (ca 40%) whereas a small part (ca 1%) corresponded to a stone-wall (1 m height) and two large rocky outcrops that provided numerous refuge sites for lizards (Supplementary material Fig. A1). Thematic categories of the habitat map were defined as 'broad-leaf shrubs', 'narrow-leaf shrubs', 'rock' and 'bare soil'. In several of the ensuing analyses, we further pooled the first two categories into a single group of 'shrubs'.

Radio-telemetry, lizard territory and plant sampling

Telemetry data on lizards

During the midday of 14 June 2005, 10 adult male lizards (range: 7.0–9.5 g) were captured in the study site and tagged with radio-transmitters (weight: 0.35 g; operating life: up to 14 d; Biotrack) dorsally attached to each lizard by means of a small back-pack. We coordinated two radio-receptors (TR-4 and hand-held two-element 'H' antennas; Telonics) to measure the bearings of each radio-tagged lizard from two pairs of tracking stations, previously set and geo-referenced. The bearings of each radio-tagged lizard were checked continuously

throughout the day, yielding approximately one measurement every 30 to 60 min. We translated bearings into locations of radio-tagged lizards (location data, hereafter) using the best biangulation method of the LOAS software (Ecological Software Solutions). To set regular trajectories, we used the adehabitat library (R Development Core Team 2010) to homogenize location data. For this purpose, we only retained locations sampled within half-hour intervals of a two-hour sampling time-span. For more information about the sampling procedure, see Santamaría et al. (2007).

Lizard territory use

For each lizard, we classified the study area into different areas with different territory preferences. We defined a) the home-range (i.e. the polygon enclosing the 0.95 cumulative probability of location data) and b) the core-area (i.e. the polygon enclosing the 0.50 cumulative probability of location data), and estimated them using the 'Home Range Tools' extension for ArcGis 9.0 (Rodgers et al. 2005). We used adaptive kernel density estimates based on least-squares cross-validation to choose the smoothing or 'window size' parameter (Worton 1989).

Lizard movement distances

For each location, we calculated a) the step distance (i.e. the net displacement between successive locations), b) the home-range distance (i.e. the distance from the location to the home-range's centroid) and c) the core-area distance (i.e. the distance from the location to the core-area's centroid).

Plant sampling

From 10 to 15 May 2009, we established 1095 sampling sites at random locations across the study area. At each site, we measured the presence/absence of *D. rodriguezii* plants (separately for adults and juveniles) within an area of 1.5×1.5 m. We used plant size, based on measures of maximum crown diameter and height, to discriminate between juveniles and adults (<2000 and >2000 cm^3, respectively; Rodríguez-Pérez and Traveset unpubl.). Because plant-size categories were assigned visually during the field survey, we confirmed the accuracy of such categorization by measuring height and maximum crown diameter from a subsample of 257 plants and assigning them visually to the two plant size categories. Lack of significant differences between measured and visual categories (two-way chi-square test: $\chi^2 = 0.376$; DF $= 256$; p $= 1.000$) confirmed that our method worked well (i.e. 97.5 and 82.95% of adults and juveniles were classify correctly).

Data preparation

Grid for habitat variables

We superimposed two grids onto our study site (hereafter referred to as lizard and plant grids; Supplementary material Fig. A1): a larger one in which cell size approximated the scale at which we sampled lizard movements (12.5 m, corresponding to the median error of the telemetry location data) and a smaller one in which cell size equalled the sampling scale of plants (1.5 m). Within both grids, we extracted

several habitat variables for each grid-cell, including the proportional cover of each habitat category (broad-leaf shrubs, narrow-leaf shrubs, rock, and bare soil; Supplementary material Fig. A1) and four habitat-fragmentation indices (number of shrub patches, mean size and shape of shrub patches, and mean distance among shrub patches; for descriptions and computational details, McGarigal et al. 2002).

Lizard territory use

We used a hierarchical approach to characterize lizard habitat preferences at three scales of territory use: 'home-range', 'core-area' and 'patch' (Supplementary material Fig. A2). To analyze home-range preferences, we compared the habitat characteristics of the grid-cells belonging to a given lizard's home-range with those grid-cells assumed to be equally accessible to that lizard but not included in its home-range (Supplementary material Fig. A2 left). For core-area preferences, we proceeded analogously, but comparing the grid-cells included in the home-range's core-area with those included in the home-range but outside its core-area (Supplementary material Fig. A2 middle). For patch preferences, we compared the subset of home-range's grid-cells that contained at least one lizard location with those that did not contain any (Supplementary material Fig. A2 right). For each individual lizard and territory-use scale, we transformed predicted/non-predicted and used/non-used grid-cells into presence/absence (1/0) values. We thus created three datasets of lizard preference, at the corresponding scales of territory use, each defined by the presence/absence of lizard (dependent variable) and the value of the habitat variables at each grid-cell (independent variables).

Lizard movement distances

We associated each displacement value (step, home-range and core-area distances) to grid-cell values of the habitat variables. We considered that lizard displacements may be determined by the habitat features of the start and/or the end cell. For this purpose, we constructed six datasets of lizard movement, respectively defined by the three displacement values (dependent variables) and the habitat characteristics of either the start or the end grid-cell (independent variable) at each of the three territory-use scales.

Plant presence

As in the case of lizards, we associated the identity of each grid-cell with the corresponding presences/absences of adult and juvenile plants, as well as the value of each habitat variable. We also introduced the best models for 'lizard territory use' and 'lizard movement between habitat patches' as independent variables to model plant presence. We did not include variables related to habitat fragmentation for modelling plant presence/absence because we expected this effect to be solely relevant to model territory use and movement of lizards. We thus created two datasets, respectively based on coupling habitat characteristics, lizard territory use and movements (independent variables) to the presence/absence of either adult or juvenile plants (dependent variables).

Neighbourhood variables

We used the approach proposed by Schadt et al. (2002), in which a moving-window algorithm scaled environmental

variables from the original cell value to larger neighbourhoods. We assumed that the factors that determine lizard habitat preference (territory use and movement distances) and plant presence probably act within typical neighbourhoods that do not match the corresponding sizes of their respective grids. For each lizard and plant grid-cell, we therefore created buffers with different radii (neighbourhood distances, hereafter) and calculated the average value of the habitat variables within these neighbourhoods ($n_L = 7$ and $n_P = 8$ for lizards and plants, respectively; Supplementary material Fig. A3). For each dependent variable, we created n_L and n_P datasets containing the environmental variables at increasing neighbourhood distances. In general, habitat autocorrelation increased with the neighbourhood distance (Supplementary material Fig. A3).

Data analyses

All statistical analyses were performed using generalized linear (mixed) models (GLM). For each analysis, we started from full models that included all variables that remained after preliminary variable reduction and then tested all possible subsets of these variables. To select the 'best model' among all competing models, we used the Akaike's information criterion (AIC, hereafter) score. In order to get comparable estimates between variables, we standardized habitat variables. Unless otherwise indicated, average values are reported as mean ± standard error (± 1 SE) throughout the text.

Prior to modelling lizard territory use, lizard movement distance or plant presence, we discarded highly correlated habitat (independent) variables. Whenever two variables were highly correlated ($|r| > 0.70$; Supplementary material Table A1) we selected one of them based on the AIC scores of univariate models (Supplementary material Table A2). We conducted the variable reduction procedure only for the smallest neighbourhood distance, and used the selected set of independent variables for the models with all other neighbourhood distances.

For each neighbourhood distance, GLMs fitted to dependent variables were based on either binomial distributions and logit link functions (lizard territory use and plant presence) or normal distributions and log link functions (lizard movement distance), using the glmmML (territory preference), nlme (movement distance) and glm (plant presence) libraries of R (R Development Core Team 2010). For lizard territory use and movement distances, as well as adult and juvenile presence, we included habitat variables as continuous covariates; in addition, we included the presence/absence of adult plants as a binary covariable in the model predicting juvenile presence. For lizard territory use and movement distances, we also included 'lizard individual' as random factor. We also checked the spatial autocorrelation of the residuals of the GLMs for territory use and movement distances by means of Mantel correlation tests (vegan library; R Development Core Team 2010). In this test we checked for the corresponding 'best model' if the matrix of the distances of each pair of grid-cells was independent of the matrix of the difference in the residuals of each pair of grid-cells.

In order to assess the predictive power of the lizard territory-use and plant presence models, we calculated the receiver operation characteristic (ROC) curve and the area under the ROC curve (AUC) with the PresenceAbsence library (R Development Core Team 2010); The ROC and the metrics derived from this index show the intrinsic qualities of model predictions (Boyce et al. 2002). For lizard movement distance, we obtained Pearson regression coefficients from fitted and observed values with the Hmisc library (R Development Core Team 2010).

All models were subsequently evaluated using k-fold cross-validation, a re-sampling approach to assess the robustness of measures (Hastie et al. 2009). We divided the dataset into k independent elements, and for each of them we used k-1 elements to estimate the model and the kth element to validate it (Hastie et al. 2009). For this purpose, we randomly re-sampled 100 times 67% of the original data, calculated their parameter estimates, and used the parameter estimates to obtain predicted values for the remaining 33% of data ($k = 100$; 'random C-V' hereafter). In addition, for lizard territory use and movement distance, we performed an independent cross-validation in which we considered the data-set of each individual lizard ($k = 10$) as one of the k elements ('individual C-V' hereafter). Finally, for each cross-validated model, we calculated the average and standard error of AUC or Pearson regression coefficient.

Two-dimensional habitat model for plants

To explore role of the seed disperser in shaping juvenile and adult plant distribution, we used a two-dimensional habitat model as proposed by Naves et al. (2003). Our hypothesis was that two factors may determine plant presence: dispersal by lizards allows plants to reach distant locations, whereas local habitat conditions determine seed germination, seedling establishment and plant survival. We therefore constructed two different sub-models: a dispersal sub-model, based on the spatial determinants of lizard activity (lizard territory use and movement distance), and a habitat model, exclusively related to local habitat features. Since we were interested in testing how conditions imprinted in the early stages of plant recruitment (seed dispersal plus germination/establishment conditions) cascade into subsequent demographic stages, we used our field data on the distribution of juvenile plants to calibrate each sub-model separately, and then validated their combined predictions against the distribution of juvenile and adult plants.

Calibration of each sub-model (lizard activity and local habitat conditions) was based on its cut-off thresholds, i.e. on the probability value that maximized its sensitivity and specificity using the ROC and AUC results (Boyce et al. 2002). Based on these two sub-models, we classified grid-cells into four categories: a) sites where both local habitat conditions and lizard activity predict plant presence (optimal dispersal sites), b) sites where seed dispersal is predicted based on lizard activity but local habitat conditions are unsuitable for plant growth (seed sinks), c) sites where habitat conditions are suitable for plant growth but seeds are not predicted to reach the place based on lizard activity (dispersal-limited sites), and d) sites where plant absence is predicted by both models (matrix). We then calculated the relative frequency (proportion of occupied sites) of juveniles and adults in each of these four categories, and used it to validate model's prediction

(i.e. plant absences found in category-a cells, as well as plant presences found in category-b, -c and -d, represent erroneous predictions). Note that cell abundances per category for juveniles represent the prediction error of the calibrated two-dimensional model (i.e. estimates came from the juvenile model, see above) whereas, for adult plants, they are validations.

Results

Lizard territory use

For the three different models of territory use (home-range, core-area and patch), we retained six habitat variables that were uncorrelated (Supplementary material Table A1 for cross-correlations and Supplementary material Table A2 for univariate model results): the cover (%) of broad-leaf shrubs (*BLS*), narrow-leaf shrubs (*NLS*) and rocks (*Rocks*), the area (*Area*) and shape (*Shape*) of shrub patches, and the connectivity among shrub patches (distance to the closest-neighbouring patch; *DNP*). Among the three models, the one based on the core-area provided the best fit to the data, followed by the home-range model (which resulted in a moderately–good fit) and the patch-scale (which resulted in a poor fit; Fig. 1). Hence, we will only report the results of the 'core-area' model. For information about the results of the other two models, see Supplementary material (Table A3).

Habitat aggregation scale also influenced model goodness-of-fit. Within the core-area, the best-fit model was based on habitat variables aggregated at neighbourhood distances of 75 m. At this scale, AUC values indicated good performance of the model (AUC = 0.76 ± 0.02; Fig. 1), AIC was more than 10 units smaller than for the second-best model (Supplementary material Table A3), and residuals
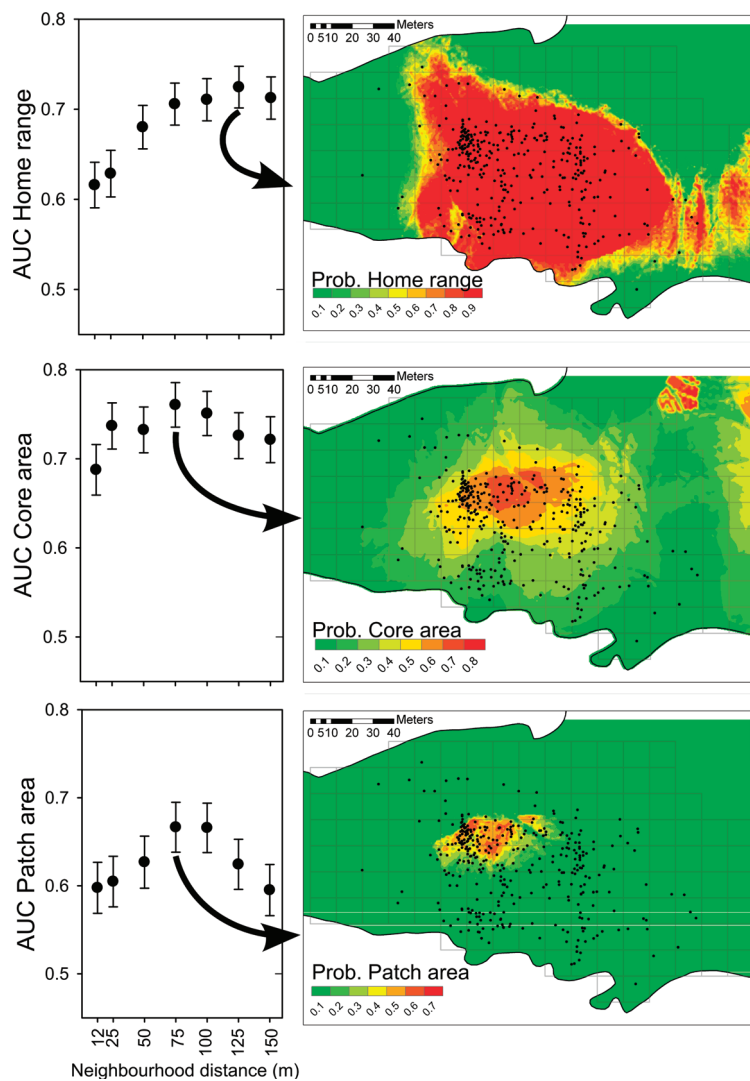

Figure 1. Model predictabilities (left panels) and prediction maps (right panels) of the probability of lizard territory use, at the home-range (upper panels), core-area (middle panels) and patch (lower panels) scales. Model predictabilities (AUC; mean ± SE) were calculated at increasing neighbourhood distances of habitat aggregation. AUC values provides a metric of the predictive power of the model that ranges between 0.5 (null predictive power) and 1.0 (perfect model; Boyce et al. 2002). Prediction maps were calculated from the model parameters that provided the best fit of lizard territory use at each respective scale, and for the neighbourhood-distance that maximised model predictability (i.e. those with the highest AUC; black arrow). Black points represented observed lizard locations.

showed no spatial auto-correlation (Mantel correlation test: -0.061; $p = 1.000$). Lizard territory use was positively associated with *Rocks* and *BLS*, and negatively with *NLS* (Table 1). Random cross-validation of the core-area model yielded an AUC value of 0.71 ± 0.02, which indicates absence of over-fitting. In contrast, individual cross-validation resulted in consistently lower AUC values (Supplementary material Table A3), suggesting that individual lizards were the major source of variability affecting the model predictive capacity.

Lizard movement between-habitat patches

In all cases, lizard movement distance was better described by the habitat features of the end-patch than by those of the start-patch (Fig. 2). While step distance and distance to the centre of the home-range were poorly predicted by habitat variables (Supplementary material Table A4 and A5), distance from the centre of the core-area provided a better model fit (Fig. 2). The neighbourhood distance of the habitat variables that produced the best fit was identical to the one that optimized the fit for the core-area model (75 m). Movement distance from the core-area was positively associated with *Rocks*, *Shape* and *DNP* and negatively to *BLS* (Table 1).

Pearson regression coefficients of the best cross-validated model predicting lizard movements at 75 m (based on the habitat features of the end-patch; see above) was high, indicating a good predictive power (Supplementary material Table A4 and A5). The residuals of the best model showed no spatial auto-correlation (Mantel correlation test: -0.043; $p = 0.974$).

Plant presence

For the presence of juveniles and adults, we respectively retained six and five uncorrelated habitat variables (Supplementary

Table 1. Results of generalized linear models for the effect of (a) local habitat characteristics on lizard territory use at the scale of core-area and (b) the habitat characteristics of the end patch on the movement distance from the centroid of the core-area. For both models, variable estimates (mean $\pm$ SE) came from the habitat neighbourhood distances (75 m) that provided the best fit and maximised model predictability (Fig. 1). Habitat variables not shown in tables were not selected in the best model and, thus, they were non-significant ($p > > 0.05$). Estimates came from standardized variables. See Supplementary material Table A3, A4 and A5 for information on variable estimates for all other neighbourhood scales. ***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, †$p < 0.10$, NS non-significant.

(a) Territory use in the core-area

Variables	Estimate	z-value
Intercept	-1.085 ± 0.180	-6.04***
BLS	0.352 ± 0.190	1.85†
Rock	0.537 ± 0.183	2.94**
DNP	-0.455 ± 0.148	-3.08**

(b) Movement distance from the core-area

Variables	Estimate	t-value
Intercept	0.022 ± 0.055	0.401NS
BLS	-0.755 ± 0.072	-10.5***
Rock	0.202 ± 0.072	2.82**
Shape	0.189 ± 0.049	3.86***
DNP	0.185 ± 0.051	3.60***

material Table A1 and A2). For juveniles, independent habitat variables were *BLS*, *NLS* and *Rocks*, the presence/absence of adult plants, and the habitat-based predictions of lizard core-area ($Core_{75}$) and step distance from the core-area ($DistCore_{75}$), both estimated for a neighbourhood distance of 75 m. For adults, we retained the same variables as those for juveniles, but omitted the presence of adults.

Presence of both adult and juvenile plants was well predicted by our set of habitat variables. Habitat-scale effects were substantially different from that of lizard activity. The predictability of juvenile presence peaked at the smallest neighbourhood distance (1.5 m) and decreased moderately with increasing neighbourhoods, whereas the presence of adults was not affected by the neighbourhood distance, except for a strong decrease at the largest distance (150 m; Fig. 3). In both juveniles and adults, best models showed a good predictive capacity (for both the inflated and cross-validated models; Supplementary material Table A6) and little to no residual spatial autocorrelation (Mantel correlation test: 0.097, $p = 0.001$ and MCT: < 0.001, $p = 0.971$, respectively).

At 1.5 m of neighbourhood distance (i.e. best model fit), the occurrence of juvenile plants was positively associated to all independent variables (Table 2), indicating a complex combination of mechanisms. It is worth noting the significant effect of the presence/absence of adult plants – which suggests that a substantial proportion of seeds are dispersed near adult plants. The specific effect of lizard activity affected juvenile presence in a dual way: a juvenile was more likely to be present at a given location if such location was either part of the lizard core-area, or more likely to receive lizard long-distance displacements from the centre of the core-area.

The occurrence of adult plants, also at 1.5 m of neighborhood distance, was positively associated to a smaller set of independent variables: the best model only included the positive effect of *BLS*, *NLS* and $Core_{75}$ (Table 2). In this case, the variable describing lizard core-area use was the most important in the model (it had the largest standardized regression coefficient).

Two-dimensional habitat model for plants

Process-based sub-models describing juvenile presence provided parameter estimates comparable to those of the best full model (i.e. local habitat conditions + lizard dispersal; Supplementary material Table A7). The differential contribution of dispersal limitation and habitat suitability to plant occupancy was spatially structured (Fig. 4), with a central core of sites with adequate lizard visitation in which 'optimal dispersal sites' were located and 'seed sinks' (seed dispersal to inadequate habitat) were interspersed, and a periphery of 'dispersal-limited sites', in which vacant sites of suitable and unsuitable habitat were also interspersed. The comparison of the estimates provided by the full model with the observed plant presences indicates that juvenile and adult plants were predominantly located in 'optimal dispersal sites' (60.8 and 48.0%, respectively; Fig. 4), where plant presence was predicted owing to the combination of suitable habitat conditions and seed dispersal. However, the model also predicted erroneous plant absences. Amongst them, a higher proportion of juvenile and adult plants were observed in predicted

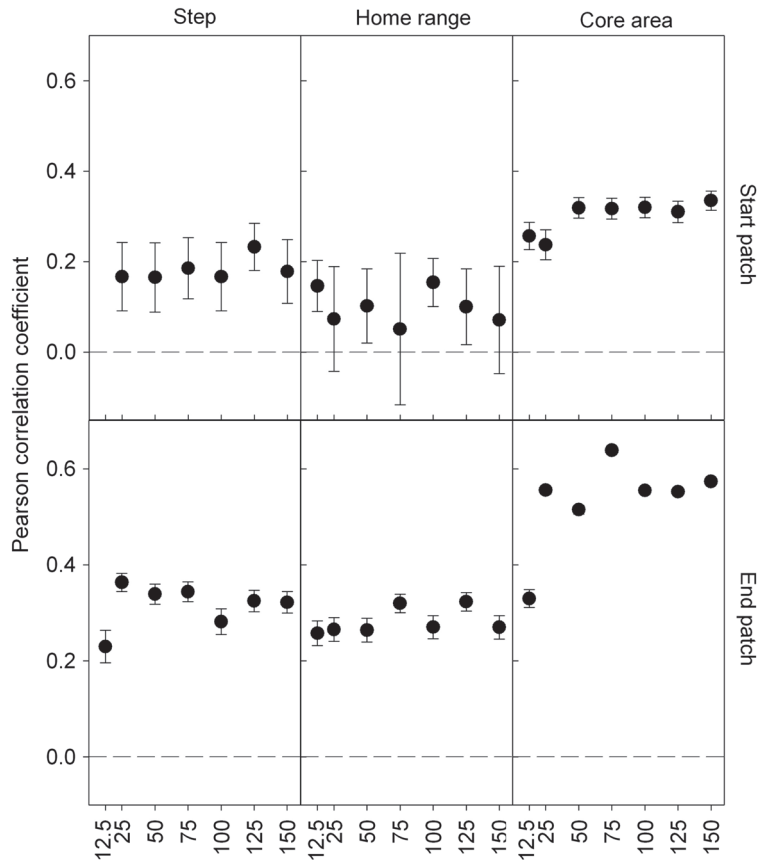Figure 2. Predictability (Pearson correlation coefficient; mean ± SE) of general linear models predicting lizard movement from habitat variables, at increasing neighbourhood distances of habitat aggregation. Upper row (three panels) shows the results of models based on habitat characteristics of the start-patch, lower row (three panels) those of the end-patch. From left to right, panels show the results of models for lizard movement (a) between successive steps, (b) from the centroid of the home-range, and (c) from the centroid of the core-area.

'seed-sink sites' (30.5 and 32.3%) than in predicted 'dispersal-limited sites' (10.3 and 2.9%) – suggesting that our model did a better job predicting seed dispersal than habitat suitability. Note also that, although the model had been calibrated solely on juveniles' data, prediction error hardly increased when it was applied to validate the distribution of adult plants.

Discussion

In this study we explored whether frugivore behaviour imprints a detectable signature on the spatial distribution of the dispersed plants. This is an important issue in ecology (Turner et al. 2001), since we try to understand here how the distribution and movement patterns of a mobile organism (i.e. with broad perception of its preferred resources) affects the distribution of a sessile organism (i.e. highly sensitive to fine-scale environmental factors). Up to now, this topic has received little attention in the literature, and only focused on the spatial distribution of predators and how they track prey (Fauchald et al. 2000, Torres et al. 2008). Plants cannot move unless they are dispersed, and consequently, understanding the spatial distribution and habitat preference of its seed disperser could help to reveal the causal relationships behind (animal-dispersed) plant spatial patterns (Russo et al.

2006, Santamaría et al. 2007, Culot et al. 2010). To this end we identified, using a scale-dependent approach, the habitat determinants of frugivore activity (the lizard *P. lilfordi*), and evaluated how they translate into the presence of a plant (*D. rodriguezii*) dispersed exclusively by that frugivore (Traveset and Riera 2005).

We found clear results. First, lizard activity strongly depended on the habitat features of the core area, the distance to such core area, and the habitat characteristics of the end-of-movement patch. Interestingly, the scale at which lizard activity was best predicted by habitat features coincided for the two measures of activity chosen (habitat use and movement distance). Second, lizard activity was a significant and reliable predictor of the presence of juvenile and adult plants, which was determined by a combination of habitat characteristics and lizard activity – indicating dispersal limitation at some good-habitat sites. Third, we found that most plants were located at 'optimal dispersal sites', where local habitat conditions were favorable and lizards provided dispersal service. However, an important proportion of plants were located at sites with high dispersal service but suboptimal local conditions, outlining both the influence of lizard activity on plant population dynamics. Thus, our study provides strong evidence that frugivore behaviour influences the spatial distribution of the plant partner, and allows us to advance predictions and management actions on the likely
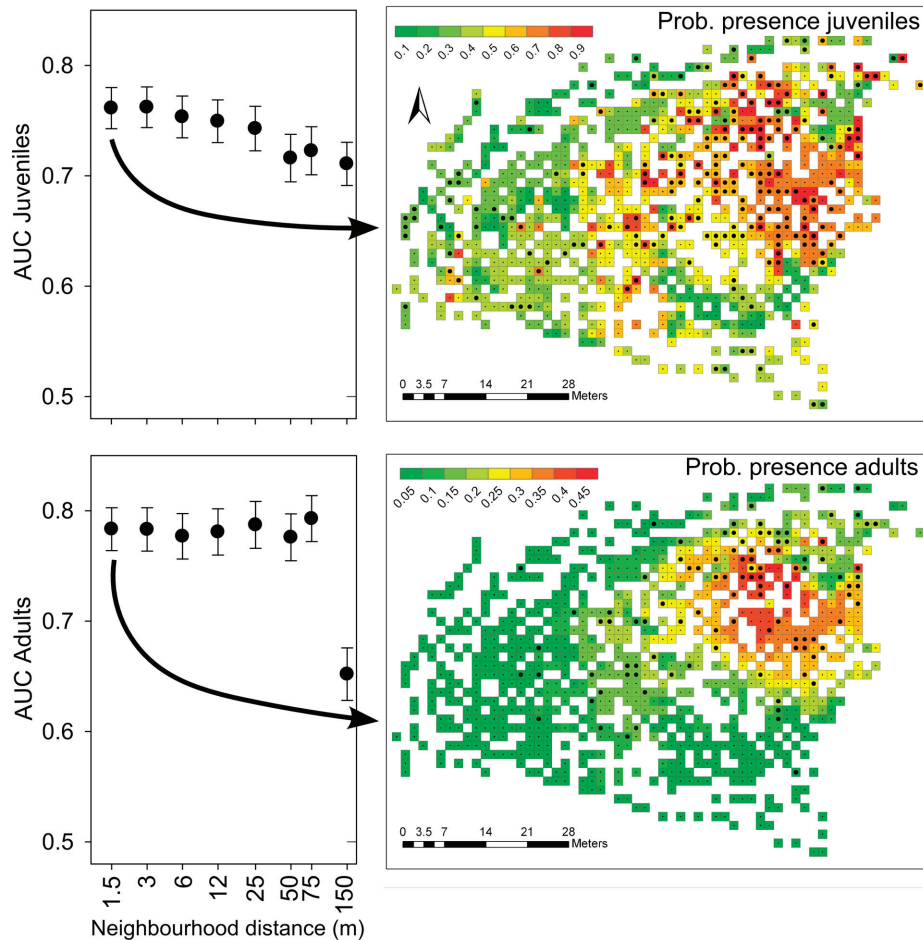
Figure 3. Model predictabilities (left panels) and prediction maps (right panels) of general linear models predicting the probability of presence of either juvenile (upper panels) or adult plants (lower panels) based on habitat variables, lizard territory use and lizard movement. Model predictabilities (AUC; mean ± SE) were calculated at increasing neighbourhood distances of habitat aggregation. Prediction maps were calculated from the model parameters that provided the best fit of lizard territory use, at each respective scale and for the neighbourhood-distance that maximised model predictability (i.e. those with the highest AUC; black arrow). Black points indicated observed presences of juveniles and adults.

fate of the plant populations in the absence of the disperser (Kaiser-Bunbury et al. 2010).

Determinants of the spatial-scale of lizard habitat use

Habitat preference in animals can be envisaged as a hierarchical spatial process, from choice of home-range to dietary items (Johnson 1980, Manly et al. 2002, Mayor et al. 2009). Consequently, the territory has to integrate broad-scale environmental features with resource availability and suitable conditions at smaller spatial scales. In our study, the lizard *P. lilfordi* showed a strong discrimination of the core area, explained by scale-dependent habitat variables. The activity of this species is probably influenced by its behaviour: it is a central-place forager, with recurrent movements to the limits of its territory and frequent revisits to the core-area (Santamaría et al. 2007). Lizards are thus likely to place their territory carefully, based on habitat features of a core-area, and be less selective in both their long-distance visits to their entire territory and the fine-scale visitation of the core-area.

When establishing its territory, animals need to make sure that all resources they require are located within reachable areas. We can therefore expect animals to base their spatial preferences not only on local habitat features, but also on the integration of information from a larger neighbourhood (Schadt et al. 2002, Naves et al. 2003, Mayor et al. 2009). In our study, habitat-based models of lizard core-area provided the best fits and predictions when habitat heterogeneity was aggregated at broad neighbourhood distances (around 75 m). At this scale, lizards responded positively to the cover of broadleaf shrubs and rocks, but negatively to larger distances to the neighbouring shrub patch. This suggests that refuge and thermoregulation habitats, and their proximity are basic to understand the choice of core-areas by this and other lizard species (Scheers and Van Damme 2002, Diego-Rasilla and Pérez-Mellado 2003, Díaz and Cabezas-Díaz 2004).

Among the lizard movement variables, movement distance from the core area was adequately predicted by the habitat characteristics of the end-patch. Hence, lizard movements were probably target-specific, dependent on 'exploratory' movements away from the centre of the core area, and based

Table 2. Results of generalized linear models for the probability of presence of (a) juvenile and (b) adult plants. For both variables, we only show the model for the habitat neighbourhood distance (1.5 m) the provided the best fit and showed the highest explanatory power (variable estimates: mean ± SE). Habitat variables not shown in tables were not selected by the best model and, thus, they were non-significant (p > > 0.05). Estimates came from standardized variables. See Supplementary material Table A6 for details on variable estimates for all other neighbourhood distances. ***p < 0.001, **p < 0.01, *p < 0.05, †p < 0.10, NSnon-significant.

(a) Presence juveniles

Variables	Estimate	z-value
Intercept	−1.727 ± 0.126	−13.7***
BLS	0.754 ± 0.162	4.66***
NLS	0.685 ± 0.145	4.44***
Rock	0.372 ± 0.084	4.72***
Adult plants	0.407 ± 0.078	5.24***
$Core_{75}$	0.769 ± 0.111	3.09**
$DistCore_{75}$	0.322 ± 0.104	6.89***

(b) Presence adults

Variables	Estimate	z-value
Intercept	−2.698 ± 0.181	−14.9***
BLS	0.577 ± 0.196	2.95**
NLS	0.477 ± 0.173	2.76**
$Core_{75}$	1.163 ± 0.151	−14.9***

on broad-scale knowledge of the territory (i.e. habitat variables aggregated at 75 m neighbourhoods). Indeed, movement distances were positively associated with rocks, patch shape and patch connectivity – indicating a potential role of landscape features facilitating movement (e.g. providing interconnected refuges) rather than associated to habitat quality of the end patch. As for the negative effect of broad-leaf shrub cover (BLS), it may reflect (in our view)

two different effects. Firstly, conspecific avoidance – because BLS is positively associated with the presence of lizard core-areas, those making long movements that avoid the core area of other lizards will probably choose destination cells with low BLS. Alternatively, long walks could be associated with poor-quality habitats – indicated by a low cover of BLS, a variable in turn associated with the high-quality habitats that define core areas. While habitats providing more resources or protection from predators may result in more tortuous movements (i.e. short step distances and frequent, less auto-correlated turns; Mueller and Fagan 2008), lower quality habitats may result instead in 'explorative walks', with higher step distances and more autocorrelated turns.

In summary, to gather information on the animal activity, we first needed to establish how the organism perceives its environment (Manly et al. 2002). Our results showed that lizards 'see' their territory at a coarse-grained scale and that their movements can be decomposed into local, tortuous, 'exploitative' walks associated with high-quality patches (core area), plus long-distance, straight, 'explorative' walks mediated by protective landscape features, but associated also with poorer-quality patches.

Plant distribution – the interactive roles of disperser preferences, habitat quality and spatial-heterogeneity

An important step in understanding how frugivores structure plant populations is to study their behaviour and activity patterns (Westcott et al. 2005, Russo et al. 2006, Culot et al. 2010). We found that lizard behaviour influenced the spatial distribution of juveniles and adult plants of the animal-dispersed plant D. rodriguezii. The dominant variable determining the presence of adults was lizard core area, followed
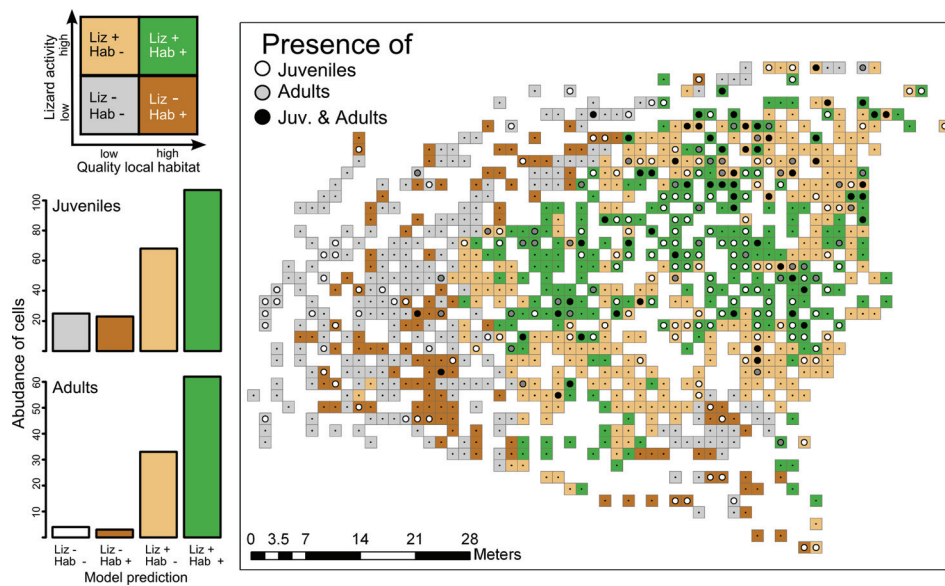

Figure 4. Two-dimensional habitat model predicting the presence of juvenile and adult plants. The upper left panel depicts a conceptual framework classifying grid-cells within a factorial space defined by lizard territory use (i.e. probability of seed dispersal) and local environment (habitat conditions). Middle and lower left panels show the abundance of cells with predicted presences of either juveniles or adult plants, respectively, for each of the four categories defined by the factorial combination of positive (+) and negative (−) values of lizard territory use and habitat conditions. The prediction map (right panel) shows the spatial distribution of the four probability-of-presence categories (see upper left panel) and the observed presence of juvenile and/or adult plants (circles).

by the cover of both shrub types (*BLS* and *NLS*). Determinants of juvenile plant presence were more complex, since they included the three variables selected at the 'best' adult model, the proximity to adults and the probability of lizard movements from the center of the core-area. The inclusion of the last variables for juveniles but not for adult plants suggest that, while lizards ensure the successful recruitment of juveniles within their core areas, seeds ingested in their 'excursions' out of such core areas can be deposited in suboptimal habitats with a lower probability to survive to adults. On the other hand, an important amount of juveniles resulted from seed deposition in optimal sites outside lizard core-areas (50%) and that suggests that long-distance dispersal (long-distance walks of lizards) could be important to connect clumps of plants (i.e. to maintain population connectivity).

It has been suggested that, in the long-term, the foraging behaviour of frugivores may shape plant distribution patterns at the landscape scale. This 'habitat shaping' process (Herrera 1985, 1988) emerges as a consequence of differences in plant recruitment resulting from seed deposition patterns. For example, we detected patches that provided suitable local conditions for plants but were located outside the area of high lizard activity (thus lacked seed-dispersal potential). However, most adults were located in sites that were suitable for both lizard activity and plant growth. This suggests that the determinants of lizard activity presented here were indeed representative of long-term lizard habitat preference. Our predictions of lizard activity were based on data from a single fruiting season and, consequently, we cannot rule out the possibility that this pattern may change from year to year (Newbold and MacMahon 2008, Calsbeek et al. 2009).

The model predicting the presence of juveniles included more fine-scale features, and at smaller neighbourhood distances, than the one fitted for adults (which were fairly scale-independent in terms of neighbourhood distance) – suggesting that juveniles are particularly sensitive to habitat variability in their close vicinity (Law et al. 2001). At the same time, both juvenile and adult plants were positively associated with sites having high shrub cover, indicating the strong association of this species with the 'canopy cover' provided by larger shrubs (e.g. *Phillyrea*, *Pistacia*) for its establishment and early survival (Traveset and Riera 2005, Rodríguez-Pérez and Traveset 2010). Theoretically, plants could increase fitness if a higher proportion of seeds were 'directly' dispersed to sites where offspring have a higher survival (Wenny and Levey 1998, Wenny 2001, Kwit et al. 2004). Indeed, lizard habitat preferences (core area) were positively correlated with a key determinant of plant seedling survival (shrub cover, see above). Although the predictive model also indicated that half of the seeds deposited by lizards during 'excursions' out of their core areas (about 20% of seeds) recruited in suboptimal open habitats (i.e. a sizable proportion of seeds were deposited outside high-quality sites), the overall prediction was that most juvenile plants (and, therefore, an even larger proportion of adults) were located in optimal dispersal sites (Fig. 4). This result stresses the importance of lizard activity to influence the plant spatial population dynamics.

In summary, the activity of the lizard *P. lilfordi* propagates into the spatial pattern of the plant *D. rodriguezii*. Adult plants strongly depend on lizard territory use and less on habitat variability, whereas juvenile plants depend on a mixture of fine-scale habitat features, lizard territory use and lizard movements. A comparison of the model predictions and the actual distribution of plants indicated that they were preferentially located in 'optimal' sites (i.e. those with frequent lizard visitation and good habitat conditions) and lizards tended to disperse seeds to such good-habitat sites – suggesting that, besides determining plant distribution, they may also tend to increase plant fitness in the long-run. A small fraction of seeds were also predicted to land outside high-density plant clumps (i.e. those preferred by lizards), stressing the importance of lizards to inter-connect plant populations. Our study therefore shows how the mechanistic understanding of animal movement and habitat use may contribute to a deeper understanding of how frugivores influence plant population dynamics, community structure and evolution (Schupp and Fuentes 1995, Wang and Smith 2002, Levine and Murrell 2003, Howe and Miriti 2004).

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