

Is the spatial pattern of a tree population in a seasonally dry tropical climate explained by density-dependent mortality?

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Abstract Spatial pattern of tropical plants is initially generated by limited seed dispersal, but the role of density-dependent and independent mechanisms as modifiers of these patterns across ontogeny is poorly understood. We investigated whether density-dependent mortality (DDM) and environmental heterogeneity can drive spatial pattern across the ontogeny of a tree in a seasonally dry tropical climate. We used Moran's I correlograms and spatial analysis by distance indices (SADIE) to assess the spatial patterns of the pre- and post-germinative stages of *Cordia oncocalyx* (Boraginaceae), an abundant tree endemic in the deciduous thorny woodland in the northeastern Brazilian semiarid region. We also used RDA to analyse the effect of DDM and environmental heterogeneity (measured by microtopography and canopy openness) in the mortality and recruitment. Seeds, seedlings, juveniles and adults showed aggregated spatial patterns; infants and immatures were randomly distributed; adults, seeds and seedlings attracted each other while adult, juveniles and immatures repulsed each other. Infant and seedling mortality rates were related to DDM and the recruitment from infant to juvenile was more influenced by spatial heterogeneity. Attraction was determined by local dispersal; repulsion was related to DDM and environment heterogeneity, which allowed the return to aggregation in adult stage. Together, these results indicated that spatial pattern can change across ontogeny, in which the initial stages are responsive to DDM and the final stages are influenced by spatial heterogeneity.

Key words: population ontogenetic stages, rainfall stochasticity, seasonally dry tropical forest, spatial association, spatial structure.

INTRODUCTION

The investigation of the spatial patterns of plant ontogenetic stages can most likely indicate which mechanisms act with greater relevance on the demography and spatial structuring of populations (Dovciak *et al.* 2001). As plant populations are composed of sessile demes, the spatial pattern of the demes results from the differential roles of mortality mechanisms on the seed rain (Suzuki *et al.* 2003). These mortality mechanisms are, in general, classified as density-dependent or independent (Silva Matos *et al.* 1999). The mechanisms of density-dependent mortality (DDM) are in accordance with the Janzen-Connell hypothesis (Janzen 1970; Connell 1971). Among the density-independent mechanisms, drought events (Couteron & Kokou 1997), and soil physico-chemical properties (Maestre *et al.* 2003) stand out. The

strength of the influence of these factors on the horizontal distribution of plants may differ not only among species, but also across ontogeny (Silvertown & Doust 1993).

Across the ontogeny, dispersal limitation mediated by the specific dispersal syndrome is considered the key initial mechanism to generate the spatial pattern of adult plants, and if this is the only generating mechanism, a concordance between the spatial pattern of seed arrival and that of seedlings and adults is to be expected (see Hubbell 1979; Condit *et al.* 2000; Nathan & Muller-Landau 2000). However, the predominance of dispersal as the main determinant of adults' spatial pattern has been questioned, since the spatial patterns of the initial stages, generated by primary dispersal, can be modified by secondary dispersal movements, by density-dependent mechanisms of mortality, or by natural or anthropic disturbances, which generate habitat spots with favourable or unfavourable conditions for germination, establishment and/or recruitment to mature stages (Wenny 2001;

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Hardy & Sonké 2004; Seidler & Plotkin 2006; Ribas-Fernández *et al.* 2009; Jara-Guerrero *et al.* 2015). For example, in an Ecuadorian seasonally dry tropical forest, Jara-Guerrero *et al.* (2015) found that habitat heterogeneity eliminated the effects of the spatial pattern generated by the dispersal syndrome and modified the spatial patterns of adults in 79% of the woody species.

In both tropical rain (Sterner *et al.* 1986; Fonseca *et al.* 2004; Ramos *et al.* 2005) and seasonally dry (San José *et al.* 1991; Skarpe 1991; Barot *et al.* 1999; Souza & Silva 2006) forests, plant spatial pattern changes from strong aggregation in the initial ontogenetic stages to random, regular, or, more commonly, decreased aggregation at the final stages. This alteration in the spatial pattern and the weak association between young and adult demes indicate that DDM is the generating process of spatial distribution across ontogeny (see Dovciak *et al.* 2001). According to the DDM mechanisms, demes settled far enough from the parent plant can avoid conspecific competition and are more likely to escape herbivorous and pathogens, thus they have the greatest chance of surviving (see Janzen 1970; Connell 1971). This would explain why adults tend to be spaced out relative to each other, resulting in a loosening of adult aggregation and a spatial dissociation between adults and younger demes (see Condit *et al.* 2000; Nathan & Casagrandi 2004; Zhang *et al.* 2007; Li *et al.* 2014).

However, other studies in those same regions – tropical rain (Hubbell 1979) and seasonally dry forests (Hay *et al.* 2000; Costa & Santos 2011) – have reported the aggregation of adults in some tree species to be greater than that found in the initial stages, contradicting the general pattern. In these cases, DDM does not explain the spatial pattern, and the increased aggregation of adults has been attributed to density-independent mechanisms, such as asexual propagation (Pare *et al.* 2009), local dispersal events (Hubbell 1979; Hardy & Sonké 2004), facilitation (Espinosa *et al.* 2015), topography and the availability of microsites with favourable conditions for survival up to maturity (Hay *et al.* 2000; Costa & Santos 2011). In addition, spatial repulsion between adults and juveniles may be a response to environmental heterogeneity (Espinosa *et al.* 2015), since different stages have different environmental requirements. However, despite the fact that the detection of DDM can be masked by the influence of habitat heterogeneity, DDM is still the predominant regulator of the spatial structure of most tropical trees, especially of abundant species (Zhu *et al.* 2010). For this reason, the recognition of how spatial distribution changes across ontogeny is a first step in the elaboration of hypotheses dealing with the mechanisms that originate the observed patterns, which can be tested in future studies (Barot *et al.* 1999).

So far, the DDM mechanisms have been considered more important generators of the spatial pattern of trees in tropical rainforests than in seasonally dry tropical forests (John *et al.* 2002; Bagchi *et al.* 2011). In dry environments, the most important processes are fire disturbance, natural drought (John *et al.* 2002; Bagchi *et al.* 2011) and positive interactions, such as mycorrhizae and facilitation (Dickie *et al.* 2007; Granda *et al.* 2014). However, John *et al.* (2002) pointed out that the apparent dichotomy between DDM and environmental heterogeneity in the regulation of spatial structuring of populations in both humid and dry climates likely results from the lack of studies on seasonally dry formations. In agreement with this view, Bagchi *et al.* (2011) argued that DDM is important in both types of environments, but environmental heterogeneity – marked by differences in soil patches, topography, water and light – could obscure the signs of DDM in tropical vegetation of dry climates. In seasonally dry formations, the populations are subjected to unpredictable variations in the temporal distribution of rain as much within a single year as between years (Chesson *et al.* 2004), as well as to changes in the vertical and horizontal light availability (Huante & Rincón 1998; Ceccon *et al.* 2006; Silveira *et al.* 2012). Therefore, the effects of DDM could be masked by environmental heterogeneity as pointed out by Bagchi *et al.* (2011), Espinosa *et al.* (2015) and Jara-Guerrero *et al.* (2015). Moreover, Dovciak *et al.* (2001) cautioned that most population studies have only analysed two or three size classes, a procedure that could mask spatial alterations across ontogeny.

We hypothesize that, on a local scale of a seasonally dry tropical forest in a semiarid climate with highly unpredictable rainfall, the spatial structuring of an abundant tree is regulated by both DDM and environmental heterogeneity. As diaspore deposition is always greater close to the parental plant (Nathan & Muller-Landau 2000), we expect that seedlings will have an aggregated pattern and will be spatially associated with adults. If the DDM mechanisms were the principal forces underpinning the spatial structuring of the population, we would expect to find greater aggregation in the initial stages and decreased aggregation in the final stages. If both DDM and environmental heterogeneity acted jointly in spatial structuring of plant demes across ontogeny, we would expect the DDM effect would be erased by environmental heterogeneity over time. This is likely to result in different spatial patterns shown by different ontogenetic stages and a different spatial structure, with gradual decrease in aggregation from early to late ontogeny, and increased aggregation at the intermediate and adult stages.

To investigate this hypothesis, we recorded the spatial pattern of the diaspore rain, the soil seed bank and five post-germinative ontogenetic stages of

Cordia oncocalyx Allemão, an abundant and endemic Boraginaceae tree in a seasonally dry tropical forest or deciduous thorny woodland, locally known as *caatinga*, a typical vegetation of the semiarid climate of northeastern Brazil. We also investigated the spatial patterns of mortality and recruitment events and the association of ontogenetic stages with one another and with environmental heterogeneity factors – rainfall, microtopography and canopy openness.

METHODS

Focal species and study area

Cordia oncocalyx Allemão (Boraginaceae) is a mesophanerophyte that occurs in shallow soils of the crystalline basement at low altitude (<500 m.a.s.l.) in the semiarid region of northeastern Brazil. Its geographic distribution is restricted to areas of deciduous thorny woodland (3–7°S and 37°–41°W), named *caatinga*, a type of woody dry savanna (Woodward *et al.* 2004). The fruit is *nuculanium* type (Spjut 1994), serotinic indehiscent, with 1.9–2.5 cm (2.2 ± 0.13) in length and 1.2–2.2 cm (1.7 ± 0.17) in width, weighting about 1.4 ± 0.3 g, which contains one to four seeds and is surrounded by a calyx that develops after fertilization and assists anemochoric dispersal (Silveira *et al.* 2005). Reproduction occurs only through seeds, and the species is exploited for the value of its wood, e.g. for energy production, landscaping, grazing and medicinal purposes (Lorenzi 2009).

We analysed the population in a fragment (5°6'58.1"S, 40°52'19.4"W, 368 m.a.s.l.) of *caatinga* in the *Reserva Natural Serra das Almas* (Serra das Almas nature reserve), municipality of Crateús, state of Ceará, northeastern Brazil. After Thornthwaite (1948), the climate is semiarid with little or no surplus water, megathermal with high potential evapotranspiration throughout the year, with index of humidity $I_h = 0$, index of aridity $I_a = 63$, index of effective humidity $I_m = -37$, and annual potential evapotranspiration $PET = 1846$ mm (1978–2008 data from the National Institute of Meteorology – INMET). The rainfall seasonality is well defined, rain is more likely to occur in Summer–Autumn (from January to May, this varies depending on the year) and is almost completely absent in Winter–Spring (from June to December). During the 1978–2008 period (data from INMET), the average annual rainfall was 683 mm, the average annual temperature was 27.7°C (from 21.2°C in March–June to 36.0°C in October–December). The *caatinga* vegetation is predominantly constituted by a therophytic herbaceous layer (Araújo *et al.* 2011) and a phanerophytic woody stratum with a density of 1795 demes ha^{-1} and a total of 25 species, amongst which *Croton blanchetianus* Baill., *Mimosa caesalpiniiifolia* Benth., *Croton adenocalix* Baill., *Bauhinia cheilantha* (Bong.) Steud. and *Cordia oncocalyx* Allemão are the five most abundant (Costa & Araújo 2012).

Data collection

To investigate how the spatial pattern changes across ontogeny, we collected data on the diaspore rain, soil seed bank and on the post-germinative ontogenetic stages. We

classified demes within the population into five stages: (i) seedling – orthotropic stalk with cotyledons, (ii) infant – orthotropic stalk without cotyledons, (iii) juvenile – stalk with first order plagiotropic branches, (iv) immature – stalk with second order branches and (v) adult – branches of the third or higher order, with or without the presence of flowers or fruit, that is, virgin and reproducer individuals (see details in Silveira *et al.* 2012). From April 2009 to April 2011, we monthly recorded the number of *C. oncocalyx* plants in each ontogenetic stage, except seedlings, in a grid of 100 contiguous 10 × 10 m plots (1 ha total area). We sampled seedlings in 100 5 × 5 m sub-plots, located in one corner of each plot. Every month, we recorded the number of dead plants (missing, or disconnected from the ground, or without leaves and with a completely dry stalk) and the plants that changed stage in each plot and sub-plot. In the first survey (T0), the number of demes in each stage (N0) was the number sampled in April 2009. In April 2010 (T1) and April 2011 (T2), the number of demes in each stage was calculated by the formula: $N_{ts} = n + i - o$, where: N_{ts} is the number of demes sampled at time t in each stage s , n is the number of demes in stage s in the previous year, i is the number of demes recruited to the stage s , and o is the number of demes that left stage s to the next stage due to death or recruitment.

To collect the seed rain, we numbered the plots from 1 to 100 and installed 0.5 × 0.5 m collectors suspended 10 cm above the soil in the centre of the 50 odd-numbered plots. Every month, we collected the fruits (diaspores) that had accumulated in each collector and estimated the annual production of diaspores in each plot (the fruit is indehiscent). To collect the soil seed bank, we used the 50 even-numbered plots and collected the litter and soil to a depth of 2 cm. We made two soil seed bank collections, one in December 2009 and another in December 2010, both at the end of the dry season.

To investigate the effect of environmental heterogeneity on the spatial distribution of the different stages and on the rates of mortality and recruitment, we gathered information on canopy openness and microtopography for every plot (spatial heterogeneity) and rainfall data throughout the study period. To calculate the percentage of canopy openness, we took hemispherical photographs in the centre of each one of the 100 plots, at 0.80 m above-ground. The photographs were taken when canopy cover was most dense, which occurred at the peak of the rainy season (March and April 2011). A Canon EOS5D digital camera with fisheye lens was used. We analysed the images using the software Gap Light Analyser (Frazer *et al.* 1999). Canopy openness varied from 12.3% to 39.5% (mean ± standard deviation: $20.8 \pm 5.0\%$).

To assess microtopography, we used a total station (Gowin TKS-202) and measured the elevation in each corner of every plot. Altitude was calculated by the mean elevation of the four corners of the plot. The slope was calculated as the average of the slopes between pairs of the plot corners. Convexity was measured as the altitude of the focus plot minus the mean altitude of the adjacent plots (in order to estimate this, we also calculated the relative altitude of the plots adjacent to the hectare). Convexity index varies from –1 to +1, where negative values indicate concave areas and positive values denote convex areas. The

direction of the steepest slope of the plot (aspect) was calculated in ArcMap v. 9.3 (ESRI, Redlands, CA, USA). Aspect was divided in two variables: sine and cosine. Altitude varied from 371.20 m.a.s.l. to 378.22 m.a.s.l. (mean \pm standard deviation: 376 ± 2.139 m.a.s.l.). Slope varied from 0.18% to 18.63% (mean \pm standard deviation: $5.58 \pm 4.11\%$). Convexity index varied from 0.85 to 0.98 (mean \pm standard deviation: 0.06 ± 0.36). Aspect varied from 0.66° to 332.56° (mean \pm standard deviation: $208.29 \pm 41.12^\circ$).

To investigate the influence of rainfall on death, growth and recruitment, we considered the data recorded by INMET for the study period. Rainfall was highly irregular both in quantity and frequency during the study period. For example, rainfall was above average in 2009 (1107 mm) and 2011 (847 mm), but below average in 2010 accumulating only 441 mm.

Data analysis

We described the spatial pattern of the pre- and post-germinative ontogenetic stages of *C. oncocalyx* at T0, T1 and T2 through spatial analysis and distance indices – SADIE, using the software SadieShell v1.22 (Conrad 2001). SADIE identifies clusters with counts greater and less than the mean and are indicated by v_i – patches (a positive value) and v_j – gaps (a negative value). The distance to regularity (D) is calculated using a transportation algorithm between donor (above average) and receiver (below average) sampling units. The spatial pattern is quantified by permutating the count of the dataset observed among sample units. The aggregation index (Ia) is obtained by dividing the observed D value by the mean value of the randomizations. If $Ia = 1$, the pattern is random; if $Ia > 1$, the pattern is aggregated; and if $Ia < 1$, the pattern is regular. Therefore, when $Ia > 1$, the higher the score of Ia, the higher is the level of aggregation of the sample (see Perry *et al.* 1999). With interpolation of v_i (patch) and v_j (gap), we produced kriging maps of the spatial patterns, using the software Surfer 8 (Golden Software, Inc. 2002), which allowed the identification of patches and gaps in space.

We used Moran's I correlograms to analyse the spatial patterns within distance classes with the software PASSaGE 2 (Rosenberg & Anderson 2011). This method analyses density data of each stage within different distance classes between plots, with the assumption of spatial randomness for the null hypothesis. Moran's I coefficient values range between -1 and 1 . Negative or positive values significantly different from zero (random) indicate different or similar densities, respectively, of the plots within the distance class considered (Legendre & Fortin 1989). We used 11 Euclidean distance classes and a range of 11 m chosen by rounding for all ontogenetic stages and for the diaspore rain and soil diaspore datasets. The correlograms were made in the R statistical language (R Development Core Team 2010).

We investigated spatial patterns in each stage and spatial association between stages at times T0, T1 and T2 as independent samples and performed spatial pattern and association analysis using SADIE (Tables 1 and 2). Since there was no difference in the spatial distribution between the

Table 1. SADIE analysis of spatial patterns in *Cordia oncocalyx*

Diaspores	N T0 (Ia)	N T1 (Ia)	N T2 (Ia)
Seed rain	429 (1.4*)	4 -	-
Seed bank (litter)	1330 (1.8*)	762 (1.5*)	-
Seed bank (soil)	228 (1.7*)	268 (1.8*)	-
Stages	N T0 (Ia)	N T1 (Ia)	N T2 (Ia)
Seedling	445 (2.8*)	334 (2.8*)	3317 (2.5*)
Infant	2152 (1.2 ^{ns})	2196 (1.1 ^{ns})	2050 (1.2 ^{ns})
Juvenile	86 (1.6*)	103 (1.8*)	115 (1.8*)
Immature	16 (1.0 ^{ns})	20 (1.1 ^{ns})	18 (1.1 ^{ns})
Adult	196 (2.5*)	196 (2.5*)	198 (2.5*)
Mortality	N T0 (Ia)	N T1 (Ia)	N T2 (Ia)
Seedling	-	339 (2.7*)	334 (1.8*)
Infant	-	108 (1.9*)	67 (1.7*)
Recruitment	N T0 (Ia)	N T1 (Ia)	N T2 (Ia)
Seedling to Infant	-	81 (2.1*)	0 -
Infant to Juvenile	-	21 (1.3 ^{ns})	12 (1.1 ^{ns})
Juvenile to Immature	-	4 -	0 -
Immature to Adult	-	0 -	2 -

N is the number of diaspores (fruits or seeds) and individuals (post-germinative ontogenetic stages). Seed rain and soil seed bank in 12.5 m^2 , seedling in 0.25 ha and other stages in 1.0 ha . Ia is the aggregation index, *spatially aggregated ($P < 0.05$), ^{ns} random pattern ($P > 0.05$), - insufficient data to perform analysis and - absence of data. T0: April/2009, T1: March/2010 and T2: March/2011.

three study years, we chose to present the kriging maps and association plots for a single period (the cohort at the end of 2009) for the seed rain, soil seed bank and six post-germinative stages (Figs 1 and 2). SADIE association test evaluates spatial similarity (X) based on the similarity between the aggregation indices (Ia) of two datasets and not on their numerical properties. Therefore, this technique has greater power than others to detect attraction or repulsion when present, independent of the spatial patterns of each dataset (Perry & Dixon 2002). The association index X varies from 1 (complete spatial attraction) to -1 (complete spatial repulsion), with 0 indicating spatial independence. We also tested the potential effects of canopy openness on the occurrence of stages using a SADIE association test of T2, the period in which we collected canopy openness data.

We used the number of dead demes to calculate the rate of mortality, estimated by dividing the number of dead demes counted in each month by the total number of demes at the end of each observation period. To investigate whether mortality rate (which occurred only in the seedling and infant stages) was higher in areas of high conspecific density, we performed a SADIE association test of mortality rate with the initial density of each stage. According to Janzen (1970) and Connell (1971), the mortality of saplings – equivalent to seedlings and infants in our study – is higher close to the parental plant due to pressure from

Table 2. SADIE association analysis of *Cordia oncocalyx*

Stage × Stage	X T0	X T1	X T2
Seed × Seedling	0.78*	0.75*	–
Seed × Infant	0.11 ^{ns}	0.08 ^{ns}	–
Seed × Juvenile	–0.47*	–0.34*	–
Seed × Immature	–0.49*	–0.47*	–
Seed × Adult	0.58*	0.54*	–
Seedling × Infant	0.12 ^{ns}	0.02 ^{ns}	0.03 ^{ns}
Seedling × Juvenile	–0.48*	–0.46*	–0.52*
Seedling × Immature	–0.32*	–0.34*	–0.51*
Seedling × Adult	0.69*	0.49*	0.62*
Infant × Juvenile	0.19 ^{ns}	0.32*	0.30*
Infant × Immature	–0.03 ^{ns}	–0.09 ^{ns}	–0.02 ^{ns}
Infant × Adult	–0.09 ^{ns}	–0.07 ^{ns}	–0.12 ^{ns}
Juvenile × Immature	0.28*	0.20*	0.29*
Juvenile × Adult	–0.29*	–0.44*	–0.44*
Immature × Adult	–0.09 ^{ns}	–0.19 ^{ns}	–0.11 ^{ns}
Mortality	X T0	X T1	X T2
Rate × Density			
Seedling × Initial seedling density	–	0.93*	1.00*
Infant × Initial infant density	–	0.45*	0.41*

X measure of local association, * probability less than 0.025 for significant attraction (positive value) or greater than 0.975 for significant repulsion (negative value), ^{ns} spatial independence and – absence of data. T0: 2009, T1: 2010 and T2: 2011.

predators and pathogens. For this reason, we investigated the spatial association between seedlings and infants mortality rate and initial density of seedlings and infants. Using *T*-test, we also investigated the role of rainfall variability on mortality by comparing the mortality rate recorded between years with different total rainfall.

We investigated effect of density dependence and environmental heterogeneity on the mortality and recruitment of seedlings and infants using canonical redundancy analysis (RDA; Rao 1964). We used densities of each stage to measure density-dependent mortality and both canopy openness and microtopography to measure spatial heterogeneity. Furthermore, we used spatial eigenvector mapping (SEVM) to correct for the effects of spatial autocorrelation in the regressions analyses (see Dormann *et al.* 2007). We calculated eigenvectors (spatial filters) from the distance matrix formed by the principal coordinates of neighbour matrices – PCNM (Borcard *et al.* 2004). These PCNMs eigenvectors were incorporated into the regression models as new explanatory variables. Only eigenvectors with significant values in the regression analysis ($P < 0.05$) were selected. Thus, three components were formed in the RDA variation partitioning: [a] – effect of density dependence; [b] – effect of environmental heterogeneity; and [c] – effect of the stochastic events or unmeasured environmental variables.

The proportion of variation explained by a set of variables was given as the adjusted R^2 of the explanatory variable set in the RDA, which is an unbiased estimator that corrects for the number of variables in the set (Peres-Neto *et al.* 2006). Negative fractions can occur when

explanatory variables are correlated but have strong and opposite effects on the response variable, or when explanatory variables have a weak correlation with the response variable but strong correlation with other explanatory variables that are correlated with the response variable (Peres-Neto *et al.* 2006). When the adjusted R^2 is negative for any fraction, this result is interpreted as zero (see Legendre 2008). Prior to the analysis, we tested for multicollinearity among the variables using the variance inflation factor (VIF): values >10 indicated collinearity. When two variables were collinear, one of them was excluded. We also tested the significance of each component of the partitioning using Monte Carlo permutation test. When necessary, we performed data transformation to normalize the variables. We used logit transformation for percentage data (mortality, recruitment and canopy openness) according to Warton and Hui (2011) and *z*-transformation for other variables. Finally, we tested for spatial autocorrelation of the residuals to validate our models and to confirm that the autocorrelation among variables was corrected. We used the “vegan” library (Oksanen *et al.* 2017) of the R statistical language (R Development Core Team 2010) to carry out the canonical analyses, variation partitioning and tests of significance of the fractions. PCNM eigen functions were created using SAM v.4.0 software (Rangel *et al.* 2010).

RESULTS

The spatial patterns of *C. oncocalyx* population varied between stages, but for each stage, patterns remained constant throughout the time period analysed (Table 1). The recently dispersed diaspores (seed rain) and those stored in the soil (seed bank) presented had an aggregated spatial pattern. Seedlings (first post-germinative stage), maintained the aggregated pattern of seeds, but not the infants, which presented a random spatial pattern (Table 1). In the other post-germinative stages, the pattern was found to be aggregated in juveniles and adults, but random in immatures (Table 1).

Stages with non-significant spatial structure (infants and immatures) showed random distribution in all distance classes. Conversely, stages (and diaspores) with significantly spatial structuring showed two different distribution forms: patches and linear gradient. Seeds showed distribution in patches, with maximum aggregation (positive autocorrelation) at short distances (up to 33 m). Seedlings, juveniles and adults showed distribution in linear gradients, with aggregation at short distance (up to 33 m), random pattern at intermediate distances and repulsion (negative autocorrelation) over greater distances (Fig. 1).

Seedling general mortality (in all plots) was 76% in 2009 (the rainiest study year) and 100% in 2010 (the driest study year), while infant mortality was 2% in 2009 and 15% in 2010. No mortality was recorded

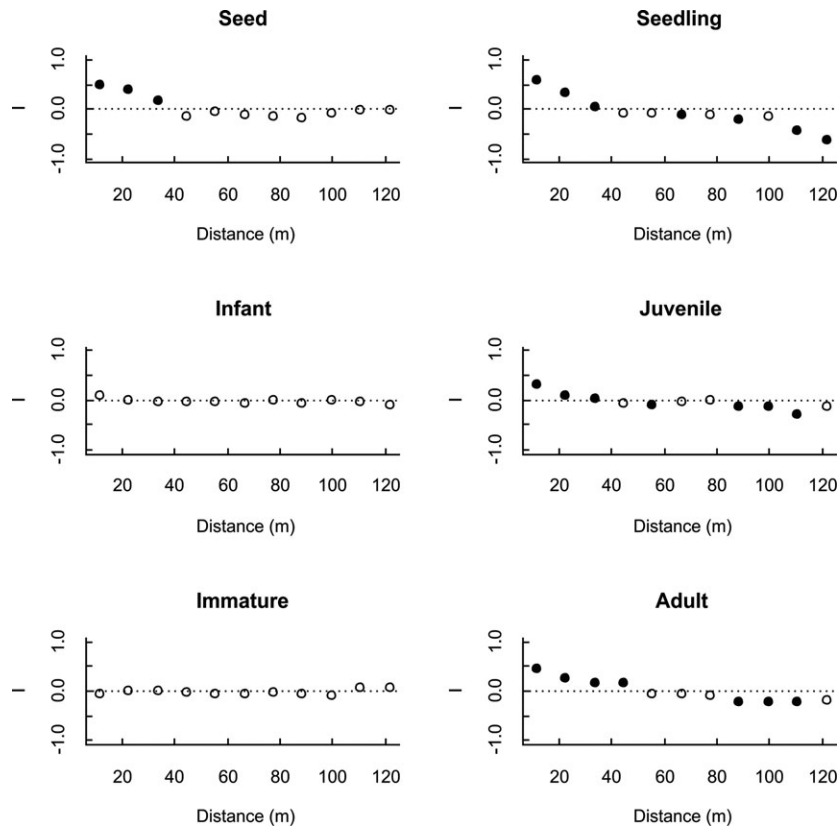


Fig. 1. Spatial autocorrelation of seed (seed rain and seed bank) and post-germinative ontogenetic stages of *Cordia oncocalyx* (cohort of the end of 2009). Filled symbols indicate 5% significance of the I value (Moran's spatial autocorrelation index) for a given distance class; empty symbols indicate non-significant values (randomness); and the dotted horizontal line indicates $I = 0$.

for the other stages. Seedling mortality had an aggregated spatial pattern (Table 1) and was density-dependent (Table 2). The mean mortality of the plots did not differ statistically ($t = 0.2281$, $P = 0.81$) between rainy (2009 – 1.107 mm) and dry (2010 – 441 mm) years. Due to spatial proximity of the plots, the spatial filters showed great influence in all analyses of variation partitioning (Fig. 2). However, when we only observed the deterministic components ([a] and [b]), we found that seedling density and spatial heterogeneity (microtopography and canopy openness) explained 7% of the total variation in seedling mortality in 2009. Although these two factors presented the similar proportion, only the initial density of seedlings (component [a] in Fig. 2A) had a significant effect, which emphasizes the role of density-dependent mortality on seedling survival. We did not analyse the variation partitioning of the seedling mortality in 2010 due to 100% seedling mortality.

Recruitment of seedling to infant was also spatially aggregated and only occurred in 2009 (the rainiest year). No seedling-to-infant recruitment occurred in the following year (2010, the driest year) due to 100% seedling mortality (Table 1). The recruitment

was explained solely by the proximity of the plots (spatial filters) while the deterministic factors (DDM and spatial heterogeneity) were not important in this process (Fig. 2B). Thus, other factors (not investigated in this study) may have influenced the spatial aggregation in the recruitment of seedling.

Infant mortality was also spatially aggregated (Table 1) and dependent on density (Table 2) and rainfall: it was significantly lower in the rainy (2009 – 1.107 mm) than in the dry (2010 – 441 mm) year ($t = -4.445$, $P = 0.00$). The total variation of infant mortality explained by all predictors also varied as a function of precipitation, from 35% in 2009 to 6% in 2010. Both density and spatial heterogeneity had an effect on infant mortality in the rainiest year (Fig. 2C). In the driest year, however, all plots appeared to have been affected equally by drought, indicating no variation caused by the spatial distribution among plots. Consequently, the deterministic factors had no influence on infant mortality (Fig. 2D).

The pattern of recruitment from infant to juvenile was random in both years (Table 1). In the same way as seen for the mortality, the total variation of

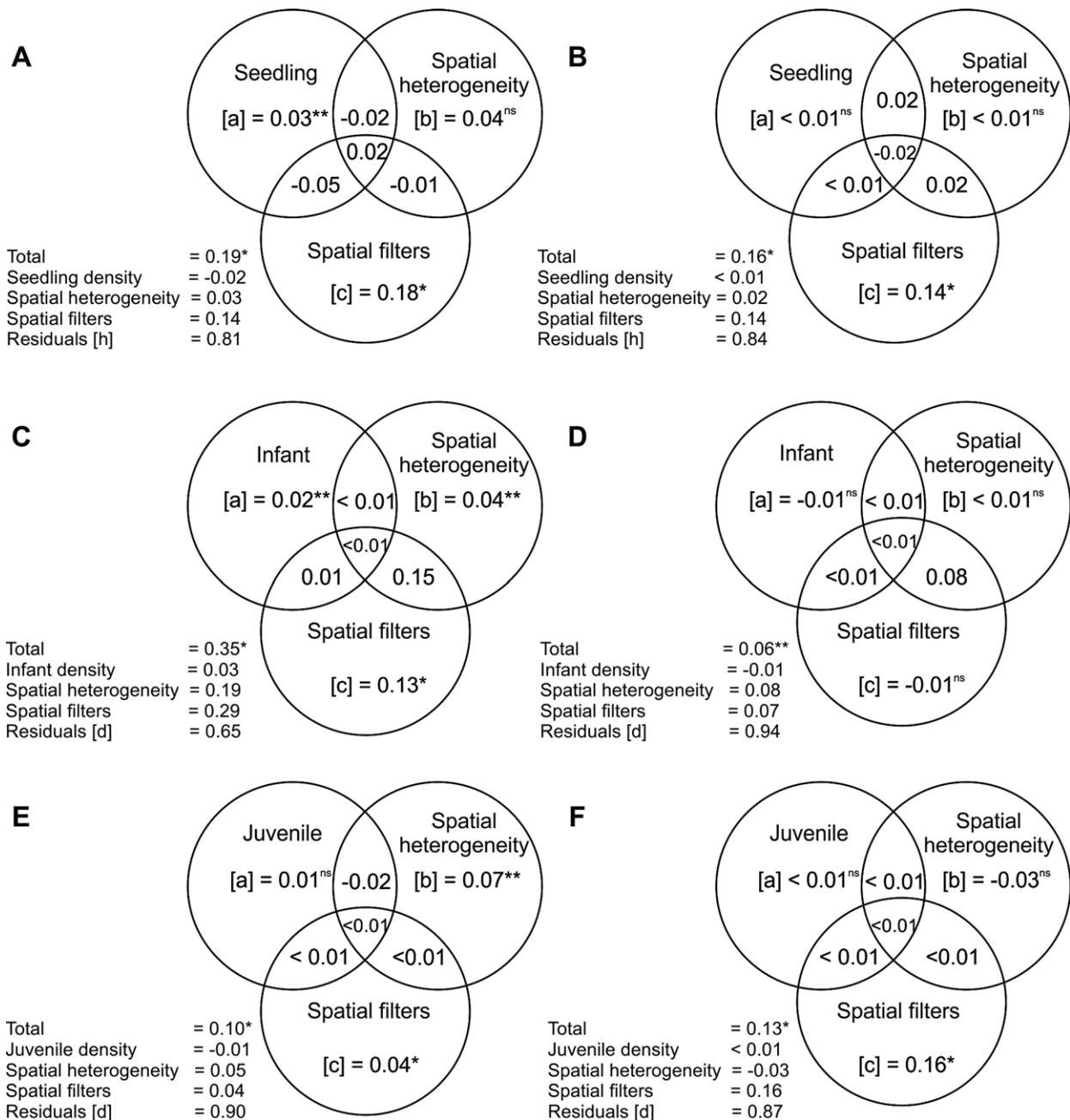


Fig. 2. Venn diagrams represent the results of RDA variation partitioning of (A) 2009 seedling mortality, (B) recruitment of seedling to infant in 2009, (C) 2009 infant mortality, (D) 2010 infant mortality, (E) recruitment of infant to juvenile in 2009 and (F) recruitment of infant to juvenile in 2010. The adjusted percentages of the unique effect of DDM [a], unique effect of spatial heterogeneity (microtopography and canopy openness variation) [b], spatial filters [c] and residuals [d] are reported in the diagrams, (ns = non-significant; ** $P < 0.1$; * $P < 0.05$).

recruitment explained by predictors varied as a function of precipitation (Fig. 2E, F). In the rainiest year, the largest proportion of variation was explained by spatial heterogeneity (Fig. 2E), suggesting that recruitment to juvenile occurred only in favourable patches. Whereas, in the driest year, none of the deterministic components presented a significant value (Fig. 2F).

The variation of the spatial pattern over time was also expressed in the associations between ontogenetic stages (Table 2). The group of recently dispersed seeds (seed rain) and those stored in the soil (seed bank) showed spatial attraction to seedlings and adults, repulsion to juveniles and immatures, and spatial independence from infants (Table 2). Seedlings showed repulsion to juveniles and

immatures, suggesting that the seedlings from which these stages originated had been recruited in different positions in the space in each reproductive event. In contrast, seedlings showed attraction to adults, indicating that during the reproductive events that occurred throughout the study period, fruit dispersal was concentrated close to the adults. Infants showed attraction to juveniles, and juveniles to immatures, indicating that certain patches could remain favourable for recruitment over a long time. However, juveniles showed repulsion to adults, suggesting that the juveniles from which the adults originated would have been, in the past, recruited in other positions in space. Immatures showed independence from adults, indicating that future adults will probably be located in different positions from those of the present adults (Table 2). These results were confirmed by kriging maps, which showed overlap of patches with higher density of adults, seeds and seedlings, and little overlap of patches with higher density of adults, juveniles and immatures (Fig. 3).

DISCUSSION

The observed attraction between *C. oncocalyx* adults, seed rain, seed bank and seedlings indicates that the aggregation and spatial association of these stages was determined by the local dispersal pattern of the diaspores, in accordance with Hubbell (1979) and Silvertown and Doust (1993). Although persistent sepals assist anemochoric dispersal of *C. oncocalyx* diaspores, their aggregation with the adults may be due to the great fruit size and weight (2.2 ± 0.13 cm in length, 1.7 ± 0.17 cm in width, 1.4 ± 0.3 g in weight), which likely limits their dispersal over long distances. Although Ribas-Fernández *et al.* (2009) reported that secondary dispersal is common in anemochoric woody plants from arid and semiarid ecosystems and argued that this mechanism may influence seedling spatial patterns, we believe this is not the best explanation for the spatial pattern of *C. oncocalyx* seedlings. Brito and de Araújo (2009) verified experimentally that this population does not have secondary dispersal. Therefore, dispersal limitation is likely to be the principal mechanism generating the initially aggregated spatial structure of *C. oncocalyx*, confirming the dispersal limitation hypothesis (Hubbell 1979; Silvertown & Doust 1993; Nathan & Muller-Landau 2000; Clark *et al.* 2007).

It is well known that both density-dependent (DDM; see Dovciak *et al.* 2001; Zhu *et al.* 2010) and independent factors (e.g. spatial heterogeneity; see Jara-Guerrero *et al.* 2015) modify the spatial pattern generated by diaspore dispersal. We found that for *C. oncocalyx* DDM is important in the initial ontogenetic stages. We observed that seed rain, seed bank,

seedlings and adults had aggregated pattern in similar spatial positions, i.e. they attracted each other. This can be interpreted as an outcome of the dispersal limitation together with the absence of secondary dispersal. However, the great decrease in the aggregation index from seedlings to infants advocates for the action of DDM. Our results of the variance partitioning analysis confirm the effect of DDM in the mortality of seedlings and infants, mainly in the rainiest year.

The role of DDM in early ontogenetic stages has been widely reported for many tropical species (Clark & Clark 1984; Sterner *et al.* 1986; San José *et al.* 1991; Skarpe 1991; Barot *et al.* 1999; Hay *et al.* 2000; Fonseca *et al.* 2004; Souza & Silva 2006). Our results indicate that density-dependent mortality (DDM) is the main mechanism generating the spatial distribution of *C. oncocalyx* infants, agreeing with the escape model of Janzen (1970) and Connell (1971). In the escape model, the higher mortality close to the progenitor favours far-away plants to be recruited, thus leading to a weak attraction or even repulsion between ontogenetically early and late demes. Once mortality is very high near the adults, it results in spatial dissociation between adults and recruits (Barot *et al.* 1999; Nathan & Casagrandi 2004). But, the spatial repulsion between adults and recruits may also be a response to environmental heterogeneity, since different stages have different environmental requirements (Espinosa *et al.* 2015). However, when environmental heterogeneity is the main process, adults are generally expected to present a higher aggregation than seedlings (Hubbell 1979; Condit *et al.* 2000), which was not the case here.

Thus, the seedlings of *C. oncocalyx* that grew far from the adults probably had greater chances of survival and recruitment to the infant stage, as the association between infant and adult, although not significant, had negative values, indicating a tendency to repulsion between these stages. Brito and de Araújo (2009) also demonstrated that the density of *C. oncocalyx* seeds was negatively correlated with the distance to the mother-plant and that the predation rate of diaspores was higher near the reproducers, reinforcing the influence of DDM mechanisms as modulating forces of the spatial pattern of *C. oncocalyx* juveniles.

However, already in the infant stage, mortality was not only influenced by density of infants, but also by drought. From the infants to the adults, spatial heterogeneity became more important than DDM. The observed random pattern of infants and immatures and the return to aggregated pattern of juveniles and adults showed that the alterations in the spatial pattern of *C. oncocalyx* differed from the gradual reduction in the aggregation expected during ontogeny. If DDM were the only force responsible

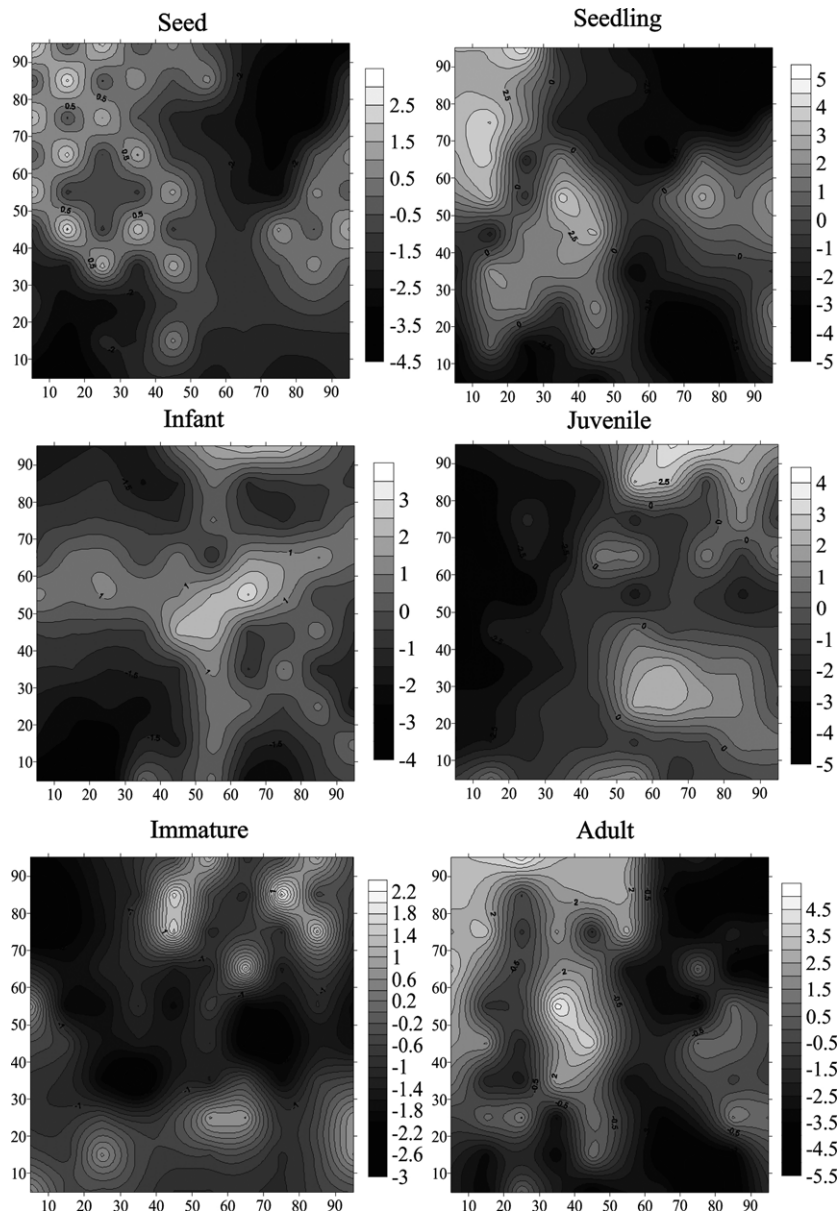


Fig. 3. Density distribution maps of seed (seed rain and seed bank) and post-germinative ontogenetic stages of *Cordia oncocalyx* (cohort of the end of 2009), drawn with the kriging technique. Light areas indicate locations with concentration of individuals (patches) and dark areas indicate the absence of individuals (gaps).

for the spatial pattern of the studied population, we would expect only a decrease in aggregation in the stages following seeds. DDM alone cannot explain these changes between aggregated and random patterns in consecutive ontogenetic stages in *C. oncocalyx* population: seedling (aggregated) to infant (random) to juvenile (aggregated) to immature (random) to adult (aggregated). Besides the occurrence of seedling-to-infant recruitment only in the rainiest year, infant-to-juvenile recruitment was influenced by environmental heterogeneity, which can also explain the change from the random pattern of infants to the

aggregated pattern of juveniles. The relation between recruitment and environmental factors emphasizes the importance of “safe sites” (*sensu* Harper *et al.* 1961) in the stage transition of plants in dry seasonally environments. The reduced density of juveniles in relation to infants also reinforces the hypothesis that recruitment to juvenile is limited. Together, these results point to our hypothesis that both DDM and environmental heterogeneity act together in the spatial structuring of the population.

In addition, the spatial pattern of the final stage (adult) returned to aggregation, which differs from

what we would expect if DDM was the only regulator of spatial pattern during ontogeny, as advocated by Janzen (1970) and Connell (1971). Rather, this alteration of the spatial pattern indicates a probable dependence on specific locations for the recruitment and survival of *C. oncocalyx* adults. For example, Jara-Guerrero *et al.* (2015) investigated the importance of spatial heterogeneity on the spatial patterns of adult trees in an Ecuadorian seasonally dry tropical forest. They found that spatial heterogeneity was the predominant mechanism that generated the spatial distribution of most species analysed, since 79% of the species had their spatial patterns modified by the effect of ecological factors, such as habitat heterogeneity. We thus suggest that factors such as light, topography, humidity and soil nutrients could determine which sites are most suitable for recruitment to maturity. Therefore, we propose future studies to elucidate the conditional factors of aggregation in the final ontogenetic stages of *C. oncocalyx*.

Our results demonstrate that DDM is not the only modifying force of the initially aggregated spatial structure that changes to random in the intermediate stages and returns to aggregate in the final stages. This change in the spatial pattern indicates that both density-dependent and independent processes influence the spatial structuring along the ontogeny of anemochoric species, as observed in *C. oncocalyx*, an abundant tree in the seasonally dry tropical vegetation of the northeastern Brazilian semiarid region.

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REFERENCES

- Araújo F. S., Costa R. C., Lima J. R. *et al.* (2011) Floristics and life-forms along a topographic gradient, central-western Ceará, Brazil. *Rodriguésia* **62**, 341–66.
- Bagchi R., Henrys P. A., Brown P. E. *et al.* (2011) Spatial patterns reveal negative density dependence and habitat associations in tropical trees. *Ecology* **92**, 1723–9.
- Barot S., Gignoux J. & Menaut J. (1999) Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology* **80**, 1987–2005.
- Borcard D., Legendre P., Avois-Jacquet C. *et al.* (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology* **85**, 1826–32.
- Brito L. B. M. & de Araújo F. S. (2009) Banco de sementes de *Cordia oncocalyx* Allemão em uma área de caatinga sobre planossolo. *Revista Caatinga* **22**, 206–12.
- Ceccon E., Huante P. & Rincón E. (2006) Abiotic factors influencing tropical dry forests regeneration. *Brazilian Arch. Biol. Technol.* **49**, 305–12.
- Chesson P., Gebauer R. L. E., Schwinning S. *et al.* (2004) Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. *Oecologia* **141**, 236–53.
- Clark D. A. & Clark D. B. (1984) Spacing dynamics of tropical rain forest tree: evaluation of the Janzen-Connell model. *Am. Nat.* **124**, 769–88.
- Clark C. J., Poulsen J. R., Levey D. J. *et al.* (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *Am. Nat.* **170**, 128–42.
- Condit R., Ashton P. S., Baker P. *et al.* (2000) Spatial patterns in the distribution of tropical tree species. *Science* **228**, 1414–8.
- Connell J. H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations* (eds P. J. Den Böer & G. R. Gradwell). Center for agricultural publications and documentation, Wageningen, The Netherlands.
- Conrad K. F. (2001) SADIEShell Version 1.22. http://www.rothamsted.ac.uk/pie/sadie/SADIE_downloads_software_page_5_2.htm.
- Costa R. C. & Araújo F. S. (2012) Physiognomy and structure of a caatinga with *Cordia oncocalyx* (Boraginaceae), a new type of community in Andrade-Lima's classification of caatingas. *Rodriguésia* **63**, 269–76.
- Costa R. C. & Santos F. A. M. (2011) Padrões espaciais de *Qualea Grandiflora* Mart. em fragmentos de Cerrado no estado de São Paulo. *Acta Botânica Brasilica* **25**, 215–22.
- Couteron P. & Kokou K. (1997) Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecol.* **132**, 211–27.
- Dickie I. A., Schnitzer S. A., Reich P. B. *et al.* (2007) Is oak establishment in old fields and savanna openings context dependent? *J. Ecol.* **95**, 309–20.
- Dormann C. F., McPherson J. M., Araújo M. B. *et al.* (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–28.
- Dovciak M., Frelich L. E. & Reich P. B. (2001) Discordance in spatial patterns of white pine (*Pinus strobus*) size-classes in a patchy near-boreal forest. *J. Ecol.* **89**, 280–91.
- Espinosa C. I., Cruz M., Jara-Guerrero A. *et al.* (2015) The effects of individual tree species on species diversity in a tropical dry forest change throughout ontogeny. *Ecography* **38**, 001–9.
- Fonseca M. G., Martini A. M. Z. & Santos F. A. M. (2004) Spatial structure of *Aspidosperma Polyneuron* in two semi-deciduous forests in southeast Brazil. *J. Veg. Sci.* **15**, 41–8.
- Frazer G. W., Canham C. D. & Lertzman K. P. (1999) *Gap Light Analyzer-GLA, Version 2.0*. Imaging software extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.

- Golden Software, Inc (2002) *Surfer Version 8.02 – Surface Mapping System*. Golden Software, Inc, Golden, Colorado.
- Granda E., Escudero A. & Valladares F. (2014) More than just drought: complexity of recruitment patterns in Mediterranean forests. *Oecologia* **176**, 997–1007.
- Hardy O. J. & Sonké B. (2004) Spatial pattern analysis of tree species distribution in a tropical rain forest of Cameroon: assessing the role of limited dispersal and niche differentiation. *For. Ecol. Manage.* **197**, 191–202.
- Harper J. L., Clatworthy J. N., McNaughton I. H. *et al.* (1961) The evolution and ecology of closely related species living in the same area. *Evolution* **15**, 209–27.
- Hay J. D., Bizerril M. X., Calouro A. M. *et al.* (2000) Comparação do padrão da distribuição espacial em escalas diferentes de espécies nativas do Cerrado, em Brasília, DF. *Rev. Bras. Bot.* **23**, 341–7.
- Huante P. & Rincón E. (1998) Responses to light changes in tropical deciduous woody seedlings with contrasting growth rates. *Oecologia* **113**, 53–66.
- Hubbell S. P. (1979) Tree dispersal, abundance, and diversity in a tropical dry forest. *Science* **203**, 1299–309.
- Janzen D. H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–28.
- Jara-Guerrero A., De la Cruz M., Espinosa C. I. *et al.* (2015) Does spatial heterogeneity blur the signature of dispersal syndromes on spatial patterns of woody species? A test in a tropical dry forest. *Oikos* **124**, 1360–6.
- John R., Dattaraja H. S., Suresh H. S. *et al.* (2002) Density-dependence in common tree species in a tropical dry forest in Mudumalai, southern India. *J. Veg. Sci.* **13**, 45–56.
- Legendre P. (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *J. Plant Ecol.* **1**, 3–8.
- Legendre P., Fortin M. J. (1989) Spatial pattern and ecological analysis. *Vegetatio*, **80**, 107–38.
- Li L., Ye W. H., Wei S. G. *et al.* (2014) Spatial patterns and associations between Species Belonging to Four Genera of the Lauraceae family. *PLoS ONE* **9**, 1–11.
- Lorenzi H. (2009) *Árvores Brasileiras: Manual de identificação e cultivo de Plantas Arbóreas Nativas do Brasil*, 5th edn. Plantarum, São Paulo.
- Maestre F. T., Cortina J., Bautista S. *et al.* (2003) Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semi-arid degraded ecosystem. *Ecosystems* **6**, 630–43.
- Nathan R. & Casagrandi R. (2004) A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *J. Ecol.* **92**, 733–46.
- Nathan R. & Muller-Landau H. C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Tree* **15**, 278–85.
- Oksanen J., Blanchet F. G., Friendly M. *et al.* (2017). *Vegan: community ecology package*. R package version 2.4-3. <https://cran.r-project.org/web/packages/vegan/vegan.pdf>
- Pare S., Savadogo P., Tigabu M. *et al.* (2009) Regeneration and spatial distribution of seedling populations in sudanian dry forests in relation to conservation status and human pressure. *Trop. Ecol.* **50**, 339–53.
- Peres-Neto P. R., Legendre P., Dray S. & Borcard D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* **87**, 2614–25.
- Perry J. N. & Dixon P. (2002) A new method for measuring spatial association in ecological count data. *Ecoscience* **9**, 133–41.
- Perry J. N., Winder L., Holland J. M. *et al.* (1999) Red-blue plots for detecting clusters in count data. *Ecol. Lett.* **2**, 106–13.
- R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. R Foundation For Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.r-project.org>.
- Ramos F. N., Silva-Matos D. M. & Santos F. A. M. (2005) Spatial distribution of seeds and juveniles of *Enterolobium glaziovii* Bentham (Leguminosae, Mimosoideae) in the Atlantic forest, Brazil. *Acta Botânica Brasileira* **19**, 609–14.
- Rangel T. F. L. V. B., Diniz-Filho J. A. F. & Bini L. M. (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography* **33**, 46–50.
- Rao C. R. (1964) The use and interpretation of principal component analysis in applied research. *Sankhyaa A* **26**, 329–58.
- Ribas-Fernández Y., Quevedo-Robledo L. & Pucheta E. (2009) Pre-and post-dispersal seed loss and soil seed dynamics of the dominant *Bulnesia retama* (Zygophyllaceae) shrub in a sandy Monte desert of western Argentina. *J. Arid Environ.* **73**, 14–21.
- Rosenberg M. S. & Anderson C. D. (2011) Passage: pattern analysis, spatial statistics, and geographic exegesis. Version 2. *Methods Ecol. Evol.* **2**, 229–32.
- San José J. J., Fariñas M. R. & Rosales J. (1991) Spatial patterns of trees and structuring factors in a trachypogon savanna of the orinoco llanos. *Biotropica* **23**, 114–23.
- Seidler T. G. & Plotkin J. B. (2006) Seed dispersal and spatial pattern in tropical trees. *PLoS Biol.* **11**, e344.
- Silva Matos D. M., Freckleton R. P. & Watkinson A. R. (1999) The role of density dependence in the population dynamics of a tropical palm. *Ecology* **80**, 2635–50.
- Silveira A. P., Araújo E. L., Araújo F. S. *et al.* (2005) Predação de frutos e germinação de sementes em *Auxemma oncocalyx* (Allemão) Baill. e *Auxemma glazioviana* Taub. In: *Estresses ambientais: Danos e benefícios em plantas* (eds R. J. M. C. Nogueira, E. L. Araújo, L. G. Willadino & U. T. M. T. Cavalcanti) pp. 416–32. MXM, Recife, Brasil.
- Silveira A. P., Martins F. R. & Araújo F. S. (2012) Are tree ontogenetic structure and allometric relationship independent of vegetation formation type? A case study with *Cordia oncocalyx* in the Brazilian Caatinga. *Acta Oecologica* **43**, 126–33.
- Silvertown W. J. & Doust J. L. (1993) *Introduction to Plant Population Biology*. Blackwell Science, Oxford.
- Skarpe C. (1991) Spatial patterns and dynamics of woody vegetation in an arid savanna. *J. Veg. Sci.* **2**, 565–72.
- Souza V. L. & Silva O. A. (2006) Estrutura e distribuição espacial de uma população de *Stryphnodendron adstringens* (Mart.) Coville em Cerrado da reserva biológica e estação experimental de Mogi Guaçu, estado de São Paulo, Brasil. *Holos* **6**, 55–69.
- Spjut R. W. (1994) *A Systematic Treatment of Fruit Types*. New York Botanic Garden, New York.
- Sterner R. W., Ribic C. A. & Schatz G. E. (1986) Testing for life historical changes in spatial patterns of four tropical tree species. *J. Ecol.* **74**, 621–33.
- Suzuki R. O., Kudoh H. & Kachi N. (2003) Spatial and temporal variations in mortality of the biennial plant, *Lysimachia rubida*: effects of intraspecific competition and environmental heterogeneity. *J. Ecol.* **91**, 114–25.
- Thorntwaite C. W. (1948) An approach toward a rational classification of climate. *Geogr. Rev.* **38**, 55–94.

- Warton D. I. & Hui F. K. C. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92**, 3–10.
- Wenny D. G. (2001) Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evol. Ecol. Res.* **3**, 51–74.
- Woodward F. I., Lomas M. R. & Kelly C. K. (2004) Global climate and the distribution of plant biomes. *Philos. Trans. Royal Soc. B* **359**, 1465–76.
- Zhang J., Hao Z., Song B. *et al.* (2007) Spatial distribution patterns and associations of *Pinus koraiensis* and *Tilia amurensis* in broad-leaved Korean pine mixed forest in Changbai Mountains. *J. Appl. Ecol.* **18**, 1681–7.
- Zhu Y., Mi X., Ren H. *et al.* (2010) Density dependence is prevalent in a heterogeneous subtropical forest. *Oikos* **119**, 109–19.