

ORIGINAL ARTICLE

Intraspecific interactions affect the spatial pattern of a dominant shrub in a semiarid shrubland: A prospective approach

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Dispersal, physical conditions and biotic interactions contribute to determine the spatial distribution of individuals in plant populations. Much of what we know has been learned from studies that retrospectively posit mechanisms presumed to have generated the observed spatial patterns. Here we present a prospective approach. We start by measuring spatial demographic effects and evaluate if they can generate observed spatial patterns. We evaluated the influence of interactions among conspecifics on vital rates, demography and spatial distribution of *Croton aff. wagneri*, a dominant shrub in dry Andean ecosystems. Recruitment, survival and growth varied in relation with distance to conspecifics neighbours and with their summed cover. We built a spatial individual-based model and simulated its population dynamics in 30 × 30 m plots for a 30-year period. We compared the predicted spatial pattern from these demographic models with that observed among plants in 16 independent plots with the same area. Simulated populations mimicked observed spatial patterns, although in plots at high elevations the simulated populations did not reproduce the observed inhibition at small scales. Observed and simulated patterns indicated differences between elevations in maximum aggregation and location of the distances with higher aggregation. We discuss how consideration of critical seed and juvenile stages and interspecific interactions could further improve our understanding of spatial pattern and recommend that these factors be considered in future models.

KEYWORDS

Andes, *Croton*, demography, Ecuador, individual-based modelling, spatial point analysis

1 | INTRODUCTION

The fine scale spatial distribution of individuals within plant populations reflects the interplay between deterministic and stochastic processes such as dispersal, local physical conditions and biotic interactions (Antonovics & Levin, 1980; Lara-Romero, Robledo-Arnuncio, García-Fernández, & Iriondo, 2014; Pereira, Martins, Sousa Menezes, & Soares Araújo, 2017; Ripley, 1987; Seidler & Plotkin, 2006). At the same time, it is well-documented that population spatial

structure itself may influence the quality and intensity of intra- and interspecific interactions, thereby affecting vital rates and population dynamics (Antonovics & Levin, 1980; North & Ovaskainen, 2007; Seidler & Plotkin, 2006). These two facts present a chicken-and-egg dilemma in which some population processes determine fine scale patterns and such patterns in turn affect population dynamics. While it is important to differentiate the influence of biotic interactions on population dynamics and spatial distribution of individual plants in order to better understand population persistence, it

has proved difficult to advance in practice due to the spatial and temporal scales involved and lack of demographic information with spatial reference (Fedriani & Wiegand, 2014; McIntire & Fajardo, 2009).

One effective approach to tackle facets of this epistemological challenge has been the use of spatial point analysis to infer the mechanisms determining the spatial pattern of plants (Wiegand & Moloney, 2014). The underlying idea is that the patterns formed by individuals in plant populations can be described with different summary functions at a wide array of spatial scales. These realized patterns can be compared with expectations from a series of “null” models corresponding to the expectations of spatial pattern according to specific biological assumptions. By doing this we can simulate processes taking into consideration plant to plant interactions, dispersal, abiotic heterogeneity or other mechanisms and compare them with the observed patterns. This approach can be considered a retrospective approach in that inference is limited to pairing a contemporary spatial pattern with a biological mechanism which, in retrospect, may have generated it. One can evaluate if biotic interactions affect the relative location of individuals, for example, to examine whether competitive processes may be responsible for regular spatial distribution for some species (Adams, 2007; Gotelli & McCabe, 2002; Jenkins, 2006) or whether facilitation between species may generate aggregated pattern in the richness of species (Gimeno et al., 2012; Haase & Pugnaire, 1996; Montesinos, Verdú, & García-Fayos, 2007).

Many interesting findings have been generated using this retrospective approach. For instance, shifts in level of aggregation according to plant size/age (ontogeny) can be interpreted as evidence of density-dependent mortality (Chacón-Labela, de la Cruz, Vicuña, Tapia, & Escudero, 2014; De la Cruz, Romao, Escudero, & Maestre, 2008; Getzin, Wiegand, & Wiegand, 2008; Lara-Romero, Gusmán, Ramón, Vélez-Mora, & Espinosa, 2017; Stoll & Bergius, 2005). Such responses can be influenced by species characteristics and by spatial scales (Guo, Wang, & Xiao, 2005; Song, Yu, Shang, Yang, & Da, 2011). The inferred effect of neighbors, conspecific or not, are integrated at scales that depend on plant size and habitat, and may change during ontogeny (Bazzaz, 1991; Espinosa, Cruz, Jara-Guerrero, Gusmán, & Escudero, 2015; Lara-Romero et al., 2017; Schupp, 1995). Unfortunately, an unequivocal connection between observed patterns and presumed processes is confounded by the possibility of interactions among factors and reciprocal feedback, which makes prediction hard and the construction of null models sometimes unfeasible.

As far as we know, there is a paucity of prospective studies that instead start by measuring the effects of the interactions at the level of individuals and then evaluate if those data can generate the observed spatial patterns. Such demonstrations will be critical to test and improve our understanding of fine scale spatial population patterns and dynamics.

In dry Andean shrublands *Croton aff. wagneri* influences community structure by sheltering coexisting subshrubs and herbs (Espinosa, Luzuriaga, de la Cruz, & Escudero, 2014; Espinosa, Luzuriaga, de la Cruz, Montero, & Escudero, 2013; Lara-Romero et al., 2017; Ramón, de la Cruz, Chacón-Labela, & Escudero, 2016). Aggregation in *Croton* varies along altitudinal gradients and with levels of grazing pressure (Espinosa et al., 2014). Previous work has indicated that facilitation and competition may have effects on *Croton*'s population dynamics and spatial structure (Lara-Romero et al., 2017; Ramón et al., 2016). However, those studies did not directly measure demographic attributes and their inferences were built indirectly by using a retrospective approaches.

We assessed variation in recruitment, survival, growth and fecundity as function of spatial and temporal variables, particularly as function of distance and density of conspecific neighbors. We used this information to develop an individual-based model to evaluate the influence of conspecific interactions, density, site and year on vital rate variation, demography and spatial distribution of *Croton*. We used this model to simulate population dynamics of *Croton* and compared the simulated spatial pattern with that observed among plants in plots with the same area. Our models evaluate the extent that the spatial outcome of demographic process as affected by neighboring conspecific location, density, year and site variation mimics observed spatial patterns. The understanding of these phenomena can help to assess the consequences of changes in factors affecting plant density and distribution such as human alteration and climatic change.

2 | MATERIAL AND METHODS

2.1 | Study system

Our study was performed in dry shrublands characteristic of southern Ecuadorian interandean valleys, at Alamala, Catamayo, Loja Province, Ecuador. This ecosystem experiences hot (24.8°C mean annual temperature), dry conditions, with an extended dry season (317 mm mean annual precipitation; 57% of it occurring between February and May; weather station at City Airport in Catamayo 2011–2015; Figure A1). Water deficit (precipitation less than double the temperature) was prevalent 10 months a year (Espinosa et al., 2013; Figure A1). The shrubland vegetation is dominated by *Croton aff. wagnerii* (henceforth *Croton*), a shrub that can reach around 1.5 m in height. The patches of *Croton* form a matrix including sparse xerophytic and spiny vegetation co-dominated by perennials such as *Lantana canescens* Kunth; *Vachellia macracantha* (Humb. & Bonpl. ex. Willd.) Seigler & Ebinger, *Bursera graveolens* (Kunth) Triana y Planch., *Colicodendron scabridum* (Kunth) Seem. and *Opuntia*

quitensis F.A.C. Weber (Espinosa et al., 2013; Sierra, 1999; Ulloa & Jørgensen, 1995).

We studied the demography of *Croton* at two sites on a private property that spans an altitudinal gradient from around 2,000 m to the valley floor at around 1,300 m and covers an area of 12 km² approx. One site was located at 1,400 m above sea level (thereafter a.s.l.) (3°59'99"S, 79°26'30.93"W) and the other at 1,700 m a.s.l. (3°59'20" S, 79°26'26"W); situated 3.8 km apart on the same slope (Figure A2). The topography is rugged with moderately steep slopes. A small number of ungulates (donkeys, cows, goats) have been maintained in the property from time to time, but their influence on vegetation structure is mostly noted further down toward the valley floor (Espinosa et al., 2013). Although these animals do not feed on *Croton* they trample seedlings and small plants and damage plant branches when wandering.

2.2 | Sampling, analysis and model design

2.2.1 | Demographic data

We monitored seedling recruitment and survival every second month at each site between June 2014 and June 2016 in 10 permanent pairs of circular plots, each of 0.5 m diameter. To locate each pair, we generated 10 random points and for each point we located one plot under the nearest canopy of *Croton* and the paired plot in the nearest neighboring open area at least 25 cm distant from the *Croton* canopy (2 sites × 10 plots × 2 types = 40 plots in total). In each plot, we placed a nail adjacent to every new seedling and measured its distance to the main stem of the nearest adult plant. These data were aggregated by intervals post recruitment for analysis because of small sample size.

We estimated seed availability in the soil at each site with the same bimonthly frequency using 10 randomly distributed pairs of 0.5 × 0.5 m square plots (2 × 10 × 2 = 40 plots). So as not to interfere with the plots used to follow seedling recruitment and survival, these were not located on the same individuals and canopy gaps. For each pair, one plot was placed under *Croton* canopy and another in open areas between canopies. On each sampling occasion, within each square plot, we randomly choose two cells using a grid of 25 units of 10 × 10 cm and collected soil core samples each of 200 cm³. None of the sampled cells was repeated within plot and plot sites were changed each year. The two bimonthly samples from each plot were mixed, bagged and transferred within 24 hr to a laboratory to separate seeds of *Croton* (diameter of ~3 mm) using a sieve (2.8 mm mesh). Seeds were counted and scored visually as either “viable” (those with no apparent damage), “damaged” or “dried-out.” For each sample, five seeds were put in Petri dishes with moist filter paper and maintained for 4 months in a chamber with a 12-hr light cycle and 25°C constant temperature to assess germination. Seeds were discarded if they got moldy.

At each site in June/July 2013 we undertook a census of all established plants (>10 cm in height) of any perennial vascular plant species within a 50 × 70 m plot (see below and Figure A2 for *Croton* plants). For each individual, we recorded the height, the longest diameter of the canopy (hereafter “length”), and its perpendicular dimension. The location of each individual in the plot was mapped (see Figure A2 for *Croton* plants) using a high-powered GPS and tripod-mounted laser distance measure (TS02-5 Total Station, Leica Geosystems, 5051 Peachtree Corners Circle #250 Norcross, GA, 30092, USA), with an estimated accuracy of <0.5 cm.

To estimate change in plant size, survival and reproductive condition we repeated the census each year from 2014 to 2016 for all *Croton* plants in five permanent subplots of variable size (50–200 m²; two and three subplots, respectively, for a total of 300 m² in each site). At each census, we randomly selected 30 of these plants to estimate the relationship between number of inflorescences and plant size (volume; elliptical area × height). In May 2013, we counted number of fruits per inflorescence and seed number per fruit from a sample of plants in the larger plots (10 inflorescences per plant, 10 fruits per inflorescence and 50 plants randomly chosen per site).

2.2.2 | Vital rates modeling

We used a model selection approach based on Akaike's Information Criteria (AICc, Burnham & Anderson, 1998; using the R package AICcmodavg; Mazerolle, 2006) to identify the most plausible generalized linear models describing vital rate variation as a function of demographic, spatial and temporal drivers. We used binomial distributions and a logit link in the models evaluating seedling and adult survival, Poisson distributions and a logarithm link for seedling count data, and negative binomial distributions and a logarithm link for counts of inflorescences and of seeds in the soil (function glm; R Core Team, 2013) and normal distributions and an identity link for individual growth data (function lm; R Core Team, 2013). We modeled the number of seedlings recruited as a function of site, and the relative distance to the nearest stem of a reproductive conspecific. We modeled seedling survival as affected by site and the proportional distance from each seedling in the interval between the main stem of their nearest reproductive conspecific plant and the dripline of the canopy of the same focal neighboring plant. We modeled adult survival and annual plant growth per site and year as a function of initial size (for each test we compared the plant height, canopy length and volume and used the best predictor) of the focal plant. Among the variables explaining the variation of final size (growth), we included a linear or quadratic response to the summed canopy area of its conspecific neighbors within a circular plot with 5 m radius centered on each focal plant. The quadratic models evaluate the possibility of nonlinear

changes in final plant size with plant crowding. We modeled the number of inflorescences as function of plant size, year and site. We modeled the total number of seeds in the soil as a function of site and sampling occasion. We used the coefficients of the most plausible model for each of these data to simulate *Croton* population dynamics.

2.2.3 | Simulation of population dynamics

We designed and implemented a spatially explicit, individual-based model to evaluate the effects of intraspecific interactions on population dynamics and spatial structure at each site (Figures 1 and 2). Our model assumes: (a) the effect of current interactions among conspecifics explain the actual spatial pattern of individuals in the populations; (b) these interactions can be simulated as an annual Monte Carlo process; (c) other abiotic and biotic effects were negligible. We started each simulation by establishing in the simulated 30×30 m arena a random number of initial plants ranging from 40 to 180, that correspond to around 3 and 15% of observed number of plants within the actual (where the demographic data were collected) 50×70 m plots (1,295 and 1,436 total plants in the sites with high and low elevation, respectively). Canopy length for each plant was drawn from a log normal distribution (logarithm of length 4.47 ± 0.41 [94.5 ± 1.51 cm] for the high elevation sites and 4.59 ± 0.45 [107.2 ± 1.57 cm] for the low elevation sites). Established simulated plants grew, reproduced and survived following the equations of plausible models describing the effect of size, neighbors, site and annual variation on these vital rates (models evaluated and their parameters are listed in Supporting Information, Tables A1–A8). Annual variation for plant growth and survival was incorporated giving equal probability for data from each year in the study. We simulated seed dispersal and seedling establishment according to models for these rates (see below and

Supporting Information). We used the information on the location of the seedlings around the nearest conspecific stem to generate a dispersal kernel, independently per each site, assuming random dispersal in any direction around this plant. *Croton* probably has a seed bank. However, because seed numbers decayed rapidly between reproductive events, germination occurred during the wet seasons overlapping with seed production, (Figure A-3), and germination rate of seeds from the soil was very low ($< 2\%$) we allocated seedlings proportionally by fecundity to reproductive plants. Simulated plants were allowed to recruit and interacted with each other for 30 simulated annual intervals. They reached a steady state determined by a ceiling, the summed canopy cover of average size adult plants that filled the neighborhood area around each focal plant (a circular plot of 5 m radius; Figure A-6). We stopped recruitment of new plants around a plant when reaching this ceiling. We completed 199 simulations for each site. At the end of each simulation plants were counted and their degree of spatial aggregation assessed. All simulations and calculations were conducted in R version 3.4.4 (R Core Team 2013; the complete code can be consulted in Supporting Information).

2.2.4 | Spatial point pattern analysis

We evaluated in 2011–2012, 16 plots (30×30 m) at two elevation levels: 8 at low elevation (between 1,400 and 1,500 m a.s.l.) and 8 at high elevation (between 1,750 and 1,900 m a.s.l.). Half of plots were located on flat ground and other half on steep slopes (approximately 27° inclination). The plots were 200 m from each other (see Ramón et al., 2016 for more information). In each plot, all of the *Croton* individuals were mapped using a compact Electronic Laser Hypsometer TruPulse 360°, which allowed us to calculate the horizontal distance, inclination and azimuth (central

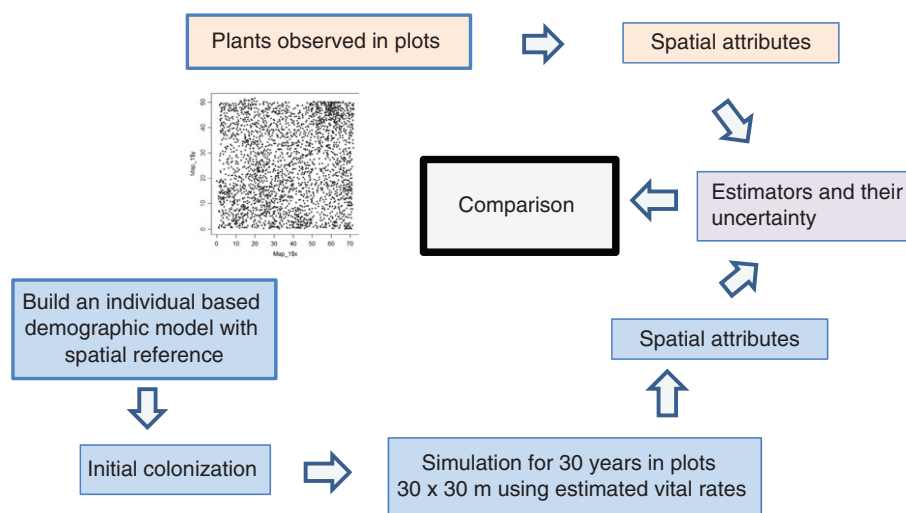


FIGURE 1 Diagram describing the steps followed to build this evaluation. We started sampling plants within plots and evaluating their spatial attributes. The steps for observed data are in pink, while those of simulated data are in blue. We obtained spatial attributes and made comparisons with simulations after 30 annual time steps ($n = 199$ simulations)

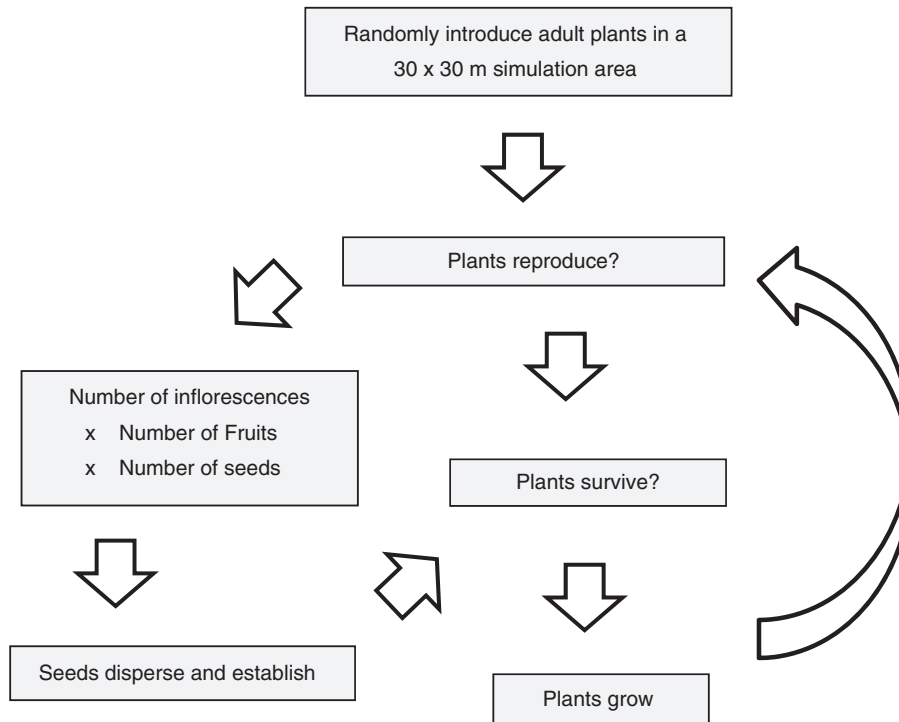


FIGURE 2 Diagram describing the algorithm of the individual-based spatially explicit model. Vital rates or processes in each box were influenced by plant size, number of neighbors, plant distance, site and year depending on the stage (see text and Supporting Information for more details)

angle) from a fixed common vertex to the rooting point of each individual with a precision of 1 cm.

We characterized the magnitude of aggregation of *Croton* in each plot using a Poisson cluster process (PCP) adjusted to each observed point pattern according to the method of minimum contrast (Diggle, 2003, Diggle, 2013; Ramón et al., 2016; using the R packages spatstat, Baddeley & Turner, 2005 and ecespa, De la Cruz, 2008). A PCP describes the formation of a spatial process in two steps. It generates a Poisson pattern of the “reference” points with intensity ρ ; then each reference point produces a number of “derived” points that follow a Poisson distribution with independent and isotropic positions around each reference point, with mean zero and *SD* σ . The aim of fitting the PCP is to estimate ρ and σ , which measure the magnitude of aggregation and to identify possible differences among populations (Jacquemyn et al. 2007; Lara-Romero et al. 2016). The theoretical K-function for a PCP given by Cressie (1991) is:

$$K(r; \rho, \sigma) = \pi r^2 + \frac{1 - e\left(-\frac{r^2}{4\sigma^2}\right)}{\rho}$$

where r is the radius of the circle (distance) defined in the K-function (Ripley, 1976). In this way for each random subplot the model is defined by two parameters: ρ , the density of aggregates (cluster centers), and σ , the average distance of a plant to the center of its cluster (Seidler & Plotkin, 2006). If the value of σ exceeds the width of the parcel or ρ exceeds plant density, it can be considered as a random distribution. We present the L-function in the y-axis for interpretation

purposes, where $L(r) = \sqrt{K(r)/\pi} - r$ is a standardized version of $K(r)$ (Besag, 1977).

We measured the level of spatial aggregation of *Croton* plants for each 1 of 199 simulated plots in each elevation and for the 16 observed plots (each of 30 × 30 m). For each observed plot, we obtained a mean observed $L(r)$ and test if this one was inside of simulation envelopes. We used a goodness-of-fit (GoF) to assess departures of mean observed $L(r)$ curves from the simulated demographic model (Loosmore and Ford 2006, Perry et al. 2006). This test was calculated over a range of 0–8 m; the maximum considered prudent for a 30 m plot size according to Baddeley, Rubak, and Turner (2015). We assessed the GoF with respect to three functionally important ranges: 0–0.5 m that defined the area under the canopy of most plants, 0.5–1.5 m that corresponded to the area of bare soil around most plants that was typically not occupied by neighbors, and 1.5–8 m that corresponded to the area of most interaction among plants in the plot.

3 | RESULTS

3.1.1 | Species attributes and vital rate variation

Croton accounted for 23 and 26% of all vascular plant stems (7,394 and 8,208 stems/ha for *Croton*) and 36 and 64% of the total vascular plant cover in the high and low elevation demography sites, respectively. *Croton* vital rate variation was affected by neighboring plant density and varied among months, years and sites (models and their parameters are listed in Tables A1–A8).

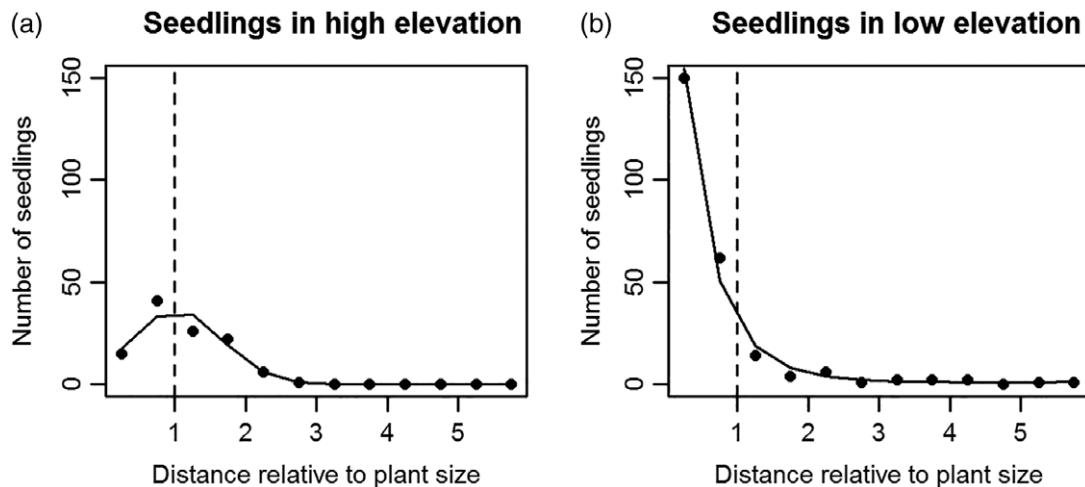


FIGURE 3 Observed *Croton* seedlings per m² at the high elevation site and the low elevation site, respectively, as a function of the proportional distance to the nearest canopy edge (drip line, marked by the dashed vertical line) of an adult conspecific

The total number of *Croton* seeds in the soil was higher in the low elevation site, inside the canopy of the plants and after the reproductive events associated with the rainy season in March 2014 and March–April 2015 (800–3,000 total seeds/m² and \bar{x} ~400–650 visually viable seeds/m²) and decreased during the dry months (100–1,000 total seeds/m² and \bar{x} ~20–200 visually viable seeds/m²). Overall germination of visually viable seeds in laboratory conditions was low (~1%) regardless of time of collection from the soil, year or site.

Seedling recruitment from soil-stored seed tended to coincide with reproductive events. Presumably both processes respond to available moisture, though only in the site with high elevation was the peak of recruitment clearly associated with the highest moisture (Figure A-3). Most observed *Croton* seedlings recruited inside of the canopy of adult plants (83% of 263 total seedlings and 80% of 111 total seedlings, respectively, for the study sites with high and low elevation). Seedling recruitment was at its maximum near the canopy drip line (using the largest diameter as reference) in the high elevation site but close to the center of the plants in the site with the low elevation (Figure 3).

Seedling survival during the first 2 months following recruitment, and under relatively moist conditions, was around 0.6–0.8 (Figure 4, Tables A-1 and A-2). During these first 2 months, there was no evidence of significant effect of site or distance to nearest adult plant. Under drier conditions in the next 2 months seedlings survived better under the canopy at the low elevation site and farther from the nearest adult in the high elevation site. During the next 4–6 and 6–8 bimonthly intervals, we found evidence of an effect of site and a weak effect of location on survival with conditions more favorable first at the high elevation site and then reversed to the low elevation site. Six to eight months after recruitment average survival probability decreased to 0.4 and its variance increased. Across both sites sample size was too small to build any meaningful models in months 8–12,

so the site averages were used for modeling survival in this interval.

Adult plant survival was generally high (>90%) except for small plants and in 2015 (Tables A-5 and A-6). Growth in canopy length was highest for smaller adult plants, decreased with conspecific neighbor cover and variable among years and sites (Figure A-4, Tables A-3 and A-4). Number of inflorescences per plant increased exponentially with canopy volume and there was weak evidence that varied among years and sites (Figure A-5, Tables A-7 and A-8). There were less inflorescences per plant volume in 2014 than 2015 or 2016 and in the site with low elevation than in the site with high elevation. We did not find evidence of significant variation in the number of fruits per inflorescence (z -statistic = -1.5 ; $p = 0.14$) or seeds per fruit (z -statistic = -0.3 ; $p = 0.78$) among plants within the same site, but we found more fruits per inflorescence (mean \pm SE per site; 8.7 ± 3.7 vs., 5.5 ± 2.5 fruits, respectively, for sites with low and high elevation; z -statistic = 15.5 ; $p < 0.001$) but less seeds per fruit ($2.4 + 0.04$ vs., $2.9 + 0.01$ seeds; z -statistic = -5.1 ; $p < 0.001$) at the site with low elevation.

3.1.2 | Conspecific plant interactions and spatial pattern reconstruction

Observed plots had 821.5 ± 167.13 SE plants in the site with high elevation and 534.75 ± 90.91 SE plants in the site with low elevation, while the simulated plots had 845.48 ± 17.87 in high elevations and $1,517.63 \pm 49.02$ in low elevation. Simulated populations mimicked observed spatial pattern in same area plots but slightly exaggerated the degree of aggregation in low elevation sites (Figures 5 and A-6). We found higher variability in the low elevation plots than in high elevation plots in both observed and simulated populations. GoF analysis among the 30 m plots did not show differences in spatial structure between simulated and the mean of observed plots (Table 1), except in high elevation plots and at short distances (below 0.50 cm), where the

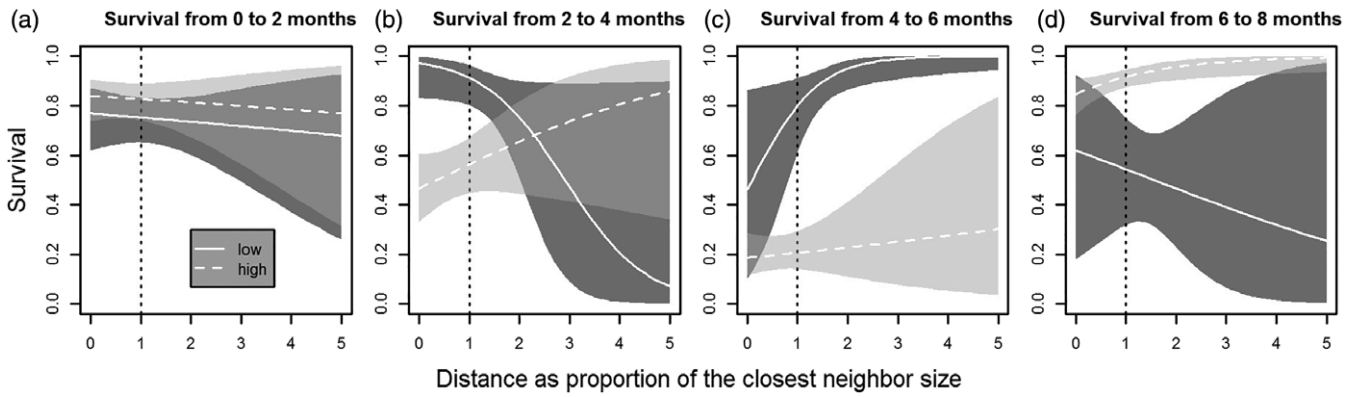


FIGURE 4 Probabilities (with 95% confidence interval [CI]) of *Croton* seedling survival at 0–2, 2–4, 4–6 and 6–8 months after germination as a function of proportional distance to the drip line of the nearest adult conspecific (vertical discontinuous line), and elevation

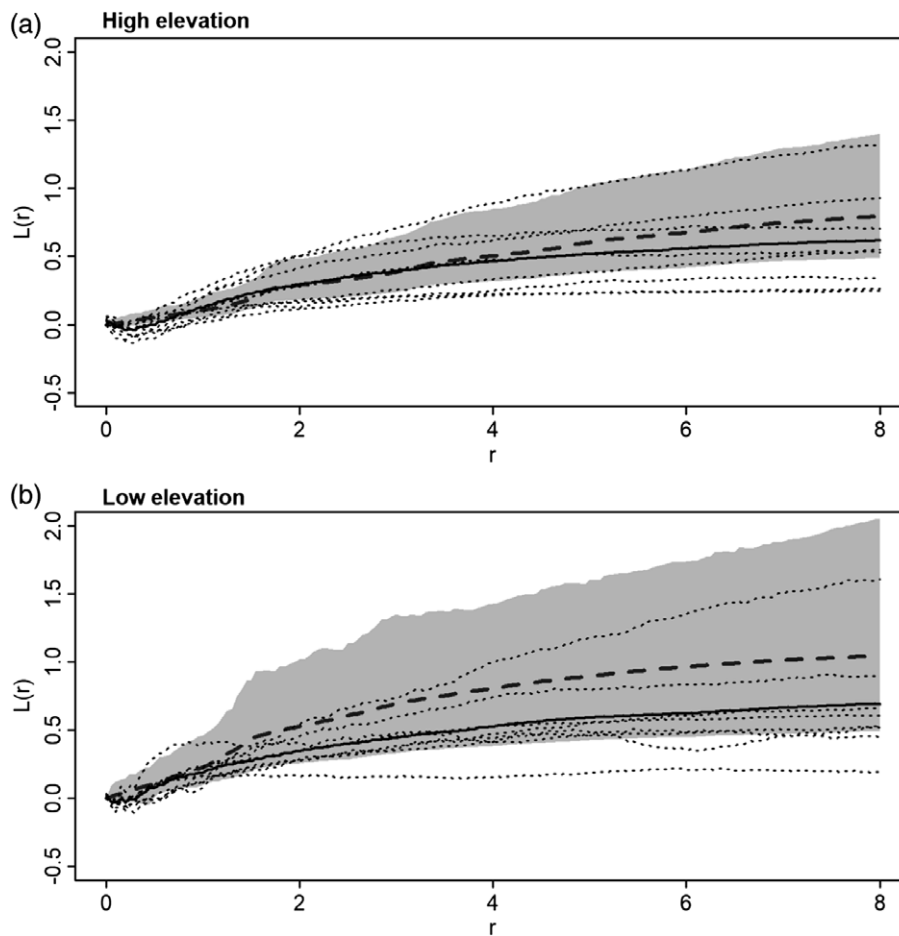


FIGURE 5 Average $L(r)$ -function for observed *Croton* point patterns and resulted from spatially explicit demographic simulation for the site with high and low elevation (demographic; $n = 199$ simulations). The mean functions are indicated as either dashed lines (observed plants) or continuous lines (for the simulated data). Grey polygons delimit their 95% confidence interval [CI] for simulated data, and dotted thin lines show the eight observed plots. The x -axis scale for r is in meters

simulated populations not reproduced the inhibition showed in observed plots.

4 | DISCUSSION

Our work indicates that relatively simple demographic models taking into consideration conspecific spatial

interactions can reproduce some attributes of the realized spatial distribution of *Croton* in contrasting conditions. In arid regions plant species occur in patches that are usually dominated by few shrub species, which act as ecosystem engineers affecting the ecosystem as a whole (Badano, Jones, Cavieres, & Wright, 2006; Jones, Lawton, & Shachak, 1994). Aguiar and Sala (1999) proposed that the demographic processes of these dominant species can

TABLE 1 Goodness-of-fit (GoF) test of mean observed $L(r)$ curves between simulated demographic models and observed plots in low and high elevations

Ranges	Low		High	
	GoF	<i>p</i> -Value	GoF	<i>p</i> -Value
0–8	13.0539	0.3433	1.9063	0.6119
0–0.5	0.0274	0.2139	0.0291	0.0149
0.5–1.5	0.1170	0.5423	0.0140	0.8109
1.5–8	12.9386	0.3383	1.8585	0.6119

Ranges are measure in meters.

determine patch dynamics and consequently plant community structure and composition. Our model included main demographic processes, recruitment, survival, growth and reproduction and the responses of all these vital rates were affected by the spatial structure of neighboring adult plants. These changes in vital rates of *Croton*, a dominant species in dry Andean ecosystems, were associated with distance to conspecifics, variable dispersal kernels, predicted varying spatial clustering patterns and differences in cluster size between sites. Previous retrospective studies in this ecosystem (Lara-Romero et al., 2017; Ramón et al., 2016) suggested that *Croton* has an aggregated spatial pattern and that cluster size is context dependent. Ramón et al. (2016) recognized higher clustering among *Croton* plants at lower elevations than in higher elevations and suggested that these differences were associated with different abiotic conditions such as altitude and slope.

Three main demographic processes have been proposed to explain clustering patterns: limited dispersal, and conspecific and interspecific interactions (i.e., nurse effects; Niering, Whittaker, & Lowe, 1963). Recruitment not only depends on primary seed dispersal, but also on multiple biotic and abiotic factors controlling seed germination and seedling establishment (Antonovics & Levin, 1980; Lara-Romero et al., 2014; Seidler & Plotkin, 2006). We found that *Croton* seedling densities in the soil were highest near or inside of the plant canopy. These findings are consistent with limited dispersal (Escudero, Giménez-Benavides, Iriondo, & Rubio, 2004). *Croton* seeds have a ballochorous dispersal syndrome and their seeds may disperse only few meters (Jara-Guerrero, de la Cruz, Espinosa, Méndez, & Escudero, 2015).

Amelioration of abiotic stress under the canopy of adult plants may favor establishment of seedlings around reproductive plants (Antonovics & Levin, 1980; Espinosa, de la Cruz, Luzuriaga, & Escudero, 2012; Fajardo & McIntire, 2011). Seedling establishment of many species appears to be more frequent under canopies of adult plants of other species, which provide a less stressful micro-environment (Ellner & Shmida, 1981). This association of seedlings and adult plants has been called “nurse plant syndrome” (Niering et al., 1963) or “nurse-protége” interaction (Cody, 1993). In these interactions, the seedlings benefit from the

micro-environment created by the adult plant with presumably little effect on the latter (a form of commensalism that is not necessarily trophic), although other authors have described facultative mutualism in nurse relationships (Gibson, Sharifi, & Rundel, 1998; Moro, Pugnaire, Haase, & Puigdefábregas, 1997; Pugnaire et al., 1996; Pugnaire, Haase, & Puigdefábregas, 1996).

Spatial patterns of recruitment and establishment of seedlings around adult plants were different between sites. In the less dense and more benign high elevation site, seedlings were concentrated in the canopy edge, while in the denser and drier low elevation site seedlings were distributed mainly inside of plant canopy. Espinosa et al. (2014) also found that *Croton* interactions change along the elevation gradient from positive interactions in populations at lower elevation, to neutral-negative in populations at higher elevations. The study site with low elevation was drier and had higher pressure by livestock than the site with high elevation. These results are consistent with the stress gradient hypothesis (Bowker, Soliveres, & Maestre, 2010; Callaway, 1997), which proposed that the strength of positive interactions increases between plants as the environment becomes less productive and more stressful.

Our simulations, which integrated significant effects of spatial distribution of conspecifics on vital rates into an individual based and spatially explicit model, generated patterns that slightly exceeded observed aggregation in the low elevation site. Neither did they reproduce the degree of inhibition observed in the high elevation site. These shortcomings may be explained by limitations in our sampling and modeling approach. We lacked data on the dynamics of *Croton* in juvenile stages and consequently our model assumed that the vital rate patterns measured on adult plants were uniformly applicable throughout ontogeny. If there is appreciable temporal variation that affects habitat suitability according to the life stage, which is further modulated by the elevational gradient, then it may have limited our ability to better reconstruct realized patterns via simulation. The dynamics of the juvenile life stages may differ from those of seedlings and adults and may have influenced the overall aggregation (Pereira et al., 2017). Our model was also blind to variation in soil and topographic variables that likely influenced plant vital rates through their effect on moisture and nutrient availability, except to the extent that they may be represented in the elevation contrast. But, we suspect that the more important limitation was that our model did not include the effects that other species may have on vital rate variation and spatial patterns in *Croton*. These results emphasize that there is more complexity than has typically been assumed in studies where a mechanistic driver of spatial structure is inferred from contemporary pattern instead of being evaluated directly.

Croton vegetation patches play an important role in community diversity and ecosystem function (Cabrera,

Cumbicus, Naranjo, Prina, & Rodríguez, 2013; Espinosa et al., 2013). *Croton* patch size and distribution can affect dispersal, recruitment and persistence of itself and many sub-dominant herbaceous and shrub species that require these environments to ameliorate strong seasonal water scarcity. Management changes such as grazing and mining that reduce cover and persistence of *Croton* populations can have strong negative effects on these ecosystems. These plant communities play a significant environmental role controlling soil erosion and reduction of flood torrents in these steep mountains and their deterioration can cause significant damage in the Andean region. Understanding the spatial dynamics of these systems can help to mitigate their deterioration and contribute to its conservation.

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