

# Environmental drivers of femaleness of an inter-Andean monoecious shrub

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## Abstract

Hetero- and conspecific interactions, nutrient availability, climate, habitat heterogeneity, and disturbances can generate variation and spatial patterns of femaleness in plants. We assessed whether year, site, plant size, plant density, and canopy area of conspecific neighbors influenced the expression and spatial aggregation of femaleness in *Croton* aff. *wagneri*, a monoecious shrub from dry shrublands of the inter-Andean valleys in Ecuador. We georeferenced in two sites (1,700 and 1,400 m.a.s.l.) in five 10 × 10 m plots, within each site, the position of each *Croton* reproductive plant during first part of flowering season in two years, and measured their height, length, and width. The femaleness index of each plant was determined by the number of female and male buds and flowers. Plant density was determined for each plot, along with the number of neighbors and the summed canopy area of conspecific neighbors (at 1.0, 2.0, and 2.5 m radius, and the five closest plants) from each focal plant. *Croton*'s femaleness at the lower elevation site was greater than at the higher elevation site and increased with plant size and with canopy of the closest five neighbors. Soil at the lower elevation site had higher temperatures and lower water content. Aggregate patterns of femaleness were found in more plots at the lower elevation site. Our results indicate that location, plant size, and canopies of conspecific neighbors of *Croton* can affect femaleness and its aggregation and support the hypothesis that femaleness can be influenced by facilitative interactions.

Abstract in Spanish is available with online material.

## KEYWORDS

*Croton*, Ecuador, Loja, monoecy, neighbors, plant size, sexual expression

## 1 | INTRODUCTION

Sexual expression in flowering plants is diverse. Species range from having individuals with perfect flowers only (hermaphroditism) to having individuals with female flowers and individuals with male flowers (dioecy; Barrett, 2002). There are polymorphic systems with different combinations of breeding system within (e.g., monoecy)

or between individuals in different species (Barrett & Hough, 2013; Elzinga & Varga, 2017). Variation of sexual expression within and between populations can significantly influence evolutionary processes as well as individual fitness and variation in reproduction along environmental gradients (e.g., Calviño & Galetto, 2010; Lázaro & Méndez, 2007; Wolfe, 1998; Yakimowski, & Barrett, 2014). Hence, identifying environmental conditions and mechanisms through

which sexual expression changes are essential in order to understand the evolution of plants (Barrett, 2002; Charlesworth, 2013; Delph, 2003).

A major component of plant reproduction is its individual spatial distribution (Bleher, Oberrath, & Böhning-Gaese, 2002; Suzuki, 2000). Factors that can generate plant spatial patterns include hetero- and conspecific interactions (Espinosa et al., 2019; Nanami, Kawaguchi, & Yamakura, 2005), nutritional requirements (Marques, Fernandes, Reis, & Assunção, 2002; Nanami, Kawaguchi, & Yamakura, 2011), environmental heterogeneity (Zuo, Zhao, Zhao, et al., 2008), breeding systems (Bleher, Oberrath, & Böhning-Gaese, 2002), and disturbances (Rayburn, & Monaco, 2011; Wolf, 2005). The influence of some of these factors on the spatial pattern of dioecious species has allowed us to understand how male and female function are distributed in natural populations (Obeso, 2002; Rayburn, & Monaco, 2011; Wolf, 2005). However, it has been scarcely evaluated if these same factors can influence spatial pattern of femaleness in monoecious species (Lázaro, & Méndez, 2007; Torices, & Méndez, 2010).

In dioecious species, differences in reproductive cost between sexes may result in differential fitness between sexes across environmental gradients. Such differences can subsequently generate spatial segregation of sexes (Bierzychudek, & Eckhart, 1988; Nuñez, Nuñez, & Kitzberger, 2008). In other words, due to high reproductive cost, females may occupy more favorable conditions with respect to spatial heterogeneity (Garbarino, Weisberg, Bagnara, & Urbinati, 2015), water availability (Ortiz, Arista, & Talavera, 2002), and/or soil fertility (Lawton, & Cothran, 2000). For example, in *Valeriana edulis* increased elevation was associated with increased water availability and female frequency, but aridification caused male frequency to increase upslope at 175 meters per decade (Petry et al., 2016). However, as far as we know, there are few studies that have addressed differential inversion in male and female function of monoecious species in environmental gradients (Aizen, & Kenigsten, 1990).

Variability in plant size can help explain sexual phenotypic expression in species with different reproductive systems (e.g., Clay, 1993; Dorken, & Barrett, 2003; Klinkhamer, de Jong, & Metz, 1997). Both in dioecious and monoecious species, herbaceous and animal-pollinated plants allocation to female function (i.e., ovules and seeds) generally increases with plant size (Bickel & Freeman 1993; Kavanagh et al. 2011; Klinkhamer, de Jong, & Metz, 1997; Obeso, 2002; Sarkissian, Barrett, & Harder 2001), while in woody and wind-pollinated plants this relationship is reversed (Bickel, & Freeman, 1993; Ganeshaiah, & Shaanker, 1991; Obeso, 2002; Pickup, & Barrett, 2011). Plant size, however, usually covaries with conspecific density (Silvertown, & Charlesworth, 2009; Weiner, 1988), and it has been suggested that both plant size and local density may influence sexual expression (Weiner, 1988). These relationships have only recently begun to be explored in monoecious species (Wang et al. 2019); therefore, it is important to continue contributing to the understanding of these interactions in monoecious species.

In southern Ecuador, the Andes mountain range forms a complicated topography with high mountains and valleys shaping the inter-Andean region (Richter 2003). In the inter-Andean region,

moisture in clouds coming from the Pacific Ocean is more rarely released as rain in its central valleys but contributes with higher wetness in the eastern sides of the mountain range as rain shadows (Harden, 2006, Young, Young, & Josse, 2011). The existence of multiple dry and wet areas has generated different microenvironments (Quintana, Girardello, Barfod, & Balslev, 2016; Richter & Moreira-Muñoz 2005). This environmental heterogeneity encourages interacting effects between topography and climate (Ramón et al. 2016). *Croton aff. wagneri* occurs in this habitat in Ecuador and is distributed throughout the inter-Andean region. Its main threats are fire, introduction of some non-native species and grazing (León-Yáñez et al. 2019). We expect that *Croton aff. wagneri* will exhibit variability in the number of male and female flowers among plants in this ecosystem in response to local stress gradients of temperature and moisture.

We investigated the influence of factors potentially affecting sexual expression of a monoecious shrub, *Croton aff. wagneri*, a dominant shrub in the inter-Andean dry scrub. We refer to sexual expression of individual plants as the ratio of male and female flowers that each individual presents. Specifically, we assessed whether year, site, plant size, reproductive plants density, and summed canopies of conspecific neighbors influence (a) the sexual expression of femaleness, and (b) the spatial aggregation of femaleness.

## 2 | METHODS

### 2.1 | Study species

*Croton aff. wagnerii* (hereafter *Croton*) is a monoecious shrub in the Euphorbiaceae family that inhabits a wide variety of habitats, mostly semi-arid and often in secondary vegetation (van Ee, Riina, & Berry, 2011). This shrub can reach 1.5 m in height. It has stellate indumentum leaves with entire margins and palmate venation (van Ee, Riina, & Berry, 2011). *Croton* plants reach reproductive maturity in 2–3 years and can survive for several years (Espinosa et al., 2019). Their inflorescences are terminal with flowers unisexual; male flowers have 12 to 14 stamens; female flowers have sepals and petals reduced; styles are bifid for a total of six stigmatic tips (van Ee, Riina, & Berry, 2011). In the inflorescence of this genus, the pistillate flowers are in the lower part and the staminate flowers in the upper part (Domínguez, & Bullock, 1989; van Ee, Riina, & Berry, 2011). Flowering of *Croton* in the study area begins in November and ends in April and exhibits variability in number of male and female flowers between and within plants in this ecosystem (Vélez-Mora et al. 2020, unpublished data). Flowers of *Croton* are visited by flies, large and small bees, syrphids and other insects with greater variety and abundance at lower elevations (Vélez-Mora, personal observation).

Our study was performed at Hacienda Alamala in dry shrublands characteristic of southern Ecuadorian inter-Andean valleys, in Catamayo, Loja Province, Ecuador. Local climate is hot (24.8°C mean annual temperature) and dry, with an extended dry season (317 mm mean annual precipitation, 57% of it occurring between February

and May) (Espinosa et al., 2019; Figure S1a). Water deficit (precipitation less than double the temperature) was prevalent 10 months a year (Espinosa, Luzuriaga, de la Cruz, Montero, & Escudero, 2013; Espinosa et al., 2019; Figure S1a). The local shrubland vegetation is dominated by *Croton*. *Croton* varies in spatial aggregation along the elevation gradient and with grazing pressure levels (Espinosa, Luzuriaga, de la Cruz, Montero, & Escudero, 2013). 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 & Planch, *Colicodendron scabridum* (Kunth) Seem. and *Opuntia quitensis* F.A.C. Weber (Espinosa, Luzuriaga, de la Cruz, Montero, & Escudero, 2013; Sierra, 1999; Ulloa, & Jørgensen, 1995). Along this environmental gradient, there is variation in air and soil temperature, moisture and soil nutrient composition (Espinosa, Luzuriaga, de la Cruz, Montero, & Escudero, 2013). The topography is rugged with moderately steep slopes (Espinosa et al., 2019; Figure S1). The study sites are inhabited by small herds of wild donkeys and horses (Espinosa et al., 2019; personal observation). During the winter season livestock load increases with cows and goats, especially at low elevation areas (Young, Young, & Josse, 2011, personal observation).

## 2.2 | Study sites and data collection

Sites were chosen based on accessibility, vegetation, and slope as examples of plant associations near the extremes of the local elevation gradient. One site was located at 1,700 a. s. l. and identified as the higher elevation site (3°58'07.90" S, 79°25'19.71" W), and the other at 1,400 a.s.l., identified as the lower elevation site (3°59'40.15" S, 79°26'31.29" W; map with location of the sites in Figure S2). At each site and within a 70 × 50 m plot, five subplots of 10 × 10 m were established in 2013 and 2016. The subplots were distributed as follows: four in the corners and one in the center with respect to the larger plot. In each plot, the spatial location of the main stem of each reproductive plant was tagged and georeferenced using a Leica FlexLine TS02 total station (Leica, Wetzlar-Germany) during the flowering season (November–December) in both 2013 and 2016. We consider a reproductive plant to be one that had female and male buds and/ or female and male flowers. During the winter season, September 2018 to March 2019, HOBO data loggers S-TMB-M006 and S-SMC-M005 (Onset, USA) were used to measure soil temperature and moisture at a depth of 10 cm, with a sampling interval of 5 min at each site which recorded 66,932 and 48,931 soil temperature and moisture samples for higher elevation site and lower elevation site, respectively.

## 2.3 | Plant attributes

To estimate plant size, plant height as well as length and width of canopy of each sampled plant were measured. Plant size was

considered as the volume of an elliptical cylinder that is consistent with the shape of *Croton*. This was calculated with the formula:

$$V = \left(\frac{a}{2}\right) \left(\frac{b}{2}\right) \cdot \pi \cdot h \quad (1)$$

where  $a$  is the length,  $b$  is the width of the canopy and  $h$  is the height of the plant. The volume of each plant was transformed to natural logarithm.

We also calculated the canopy of each plant as follows:

$$C = \left(\frac{a}{2}\right) \left(\frac{b}{2}\right) \cdot \pi \quad (2)$$

where  $a$  is the length and  $b$  is the width of the canopy of the plant. For analysis, canopy data were transformed to natural logarithm.

## 2.4 | Reproductive plant density and neighborhood composition

In November and December of 2013 and 2016, reproductive individuals were selected and counted in each 10 × 10 m subplot at the two sites with different elevation. This time interval includes at least one-third of the annual flowering of our focal species which depends on the extent of the regional rainy season. Plant density was calculated as the number of reproductive individuals in the 10 × 10 m plots (10 density values were obtained for each year). To assess influence of specific neighborhood over femaleness, we generated estimates of neighborhood composition at different distances from each focal plant with *markstat* function from R package "spatstat" v 1.57-1 (Baddeley, Rubak, & Turner, 2015). Calculated variables were as follows: (a) Number of neighbors that were within 1.0, 2.0, and 2.5 m radius (maximum radius); (b) Sum of volumes of conspecific neighbors that were at 1.0, 2.0, and 2.5 m radius (maximum radius); (c) Sum of canopies of neighbors that were 1.0, 2.0, and 2.5 m (maximum radius), and (d) Sum of volumes and canopies of the five closest neighbors.

## 2.5 | Phenotypic femaleness index ( $G_i$ )

During the flowering season (November - December) in both 2013 and 2016, five inflorescences were randomly selected on each plant of each 10 × 10 m plot in both sites (1,145 plants and 5,725 total inflorescences). Then, number of female and male buds and number of female and male flowers of each inflorescence were counted in situ and an average of female and male flowers per inflorescence was obtained from each plant. The standardized phenotypic femaleness index ( $G_i$ ) of each plant was used to estimate the sexual expression of *Croton*, according to Lloyd (1980) as follows:

$$G_i = \frac{o_i}{o_i + p_i \left( \frac{\sum o_i}{\sum p_i} \right)} \quad (3)$$

where  $o_i$  is the number of female flowers of the inflorescence and  $p_i$  is the number of male flowers of the inflorescence. The index is standardized by  $\sum o_i / \sum p_i$  representing the ratio of the total female flower number to the total male flower number of all individuals for both 2013 and 2016. A value of  $G_i$  of 1 represents plants that produce only ovules and 0 plants that produce only pollen (see also Sarkissian, Barrett, & Harder, 2001).

## 2.6 | Data analysis

To evaluate the influence of year, site, plant size, density, and canopies of conspecific neighbors over femaleness, mixed-effect models (GLMM) were used with the functions of the *lme* R package (linear mixed-effects models; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2019). Year, site, and reproductive plant density were considered as fixed factors and plot as random factor.

We measured the correlation among all independent variables using the Pearson Correlation coefficient. We avoided multicollinearity by discarding variables which had high pairwise correlation greater than 0.6 or  $-0.6$  with other independent variables (Zar, 2013). Our final data set included the following independent variables: year (2013, 2016), site (higher and lower elevation site), plant size (logarithm of volume), reproductive plant density (number of reproductive individuals per plot), sum of canopies of five closest neighbors. Akaike information criterion (AIC) was used to evaluate variable combinations (Burnham, & Anderson, 2002). All analyses were performed on the statistical platform R (R Core Team, 2019).

## 2.7 | Spatial analysis

We evaluated differences in reproductive plant density between years and sites using a generalized linear model with Poisson error distribution for number of individuals. The spatial pattern of plants was characterized with the K-function (Ripley, 1976). For a homogeneous point pattern, K-function is defined by the intensity parameter  $\lambda$  (density), hence  $\lambda K(r)$  is the expected number of points within a circle of radius  $r$  around an arbitrary point. To facilitate visual interpretation, we used the L-function (Besag, 1977), that is, square root transformed K ( $L(r) = [K(r)/\pi]^{1/2} - r$ ). Homogeneous K-functions were estimated using Ripley's isotropic edge correction (Ripley, 1978). All the functions were estimated up to 2.5 m (i.e.,  $r_{\max} = 2.5$  m). To evaluate the significance of the spatial null model, 95% simulation envelopes were computed from 399 Monte Carlo simulations of each model. We evaluated the overall fit of each model with a goodness-of-fit test using the  $u$  statistic (Diggle, Besag, & Gleaves, 1976; Loosmore, & Ford 2006). We performed spatial analyses using the R package "spatstat" v 1.57-1 (Baddeley, Rubak, & Turner, 2015).

We used a one-way ANOVA-like method (Ramón et al. 2016) to test for differences in spatial distribution of femaleness between

**TABLE 1** Results of a GLM evaluating plant density as a function of year and site

Variation source	Estimate	SE	t-value	p-Value
Site at 1,700 m (reference)	51.35	6.59	7.79	<.0001
Year 2016	22.30	7.61	2.93	.009
Site at 1,400 m	-10.50	7.61	-1.38	.185

Abbreviation: SE, standard error.

sites. We computed differences between groups setting  $w(r) = R^2$ , according to Diggle (2003). The significance of the computed statistic was evaluated with 1,000 bootstrap resamplings to analyze replicated point patterns with the R package "replicatedpp2w" (Ramón et al. 2016).

## 3 | RESULTS

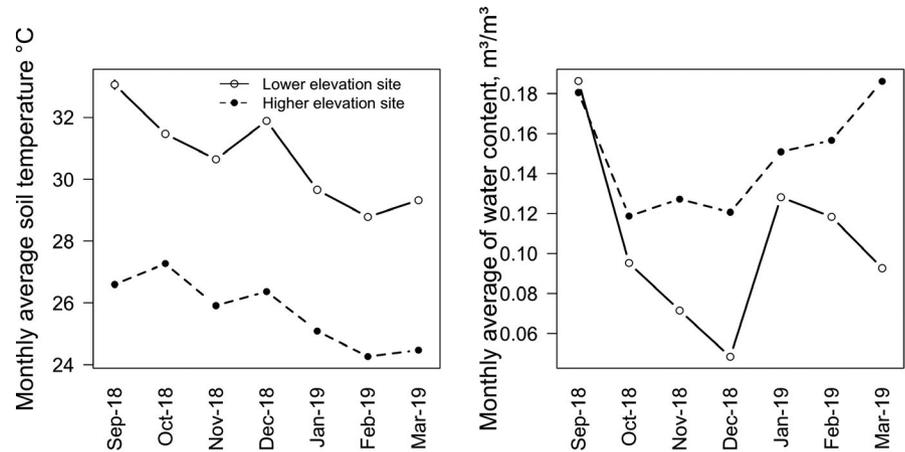
In the flowering season of 2013, we found a total of 275 reproductive plants at the higher elevation site (total of individuals of five plots) and 186 at the lower elevation site while in the flowering season of 2016 we found 350 reproductive plants at the higher elevation site and 334 at the lower elevation site. Average reproductive plant density was 55.0 individuals/100 m<sup>2</sup> (SE = 1.92) at the higher elevation site and 37.2 individuals/100 m<sup>2</sup> (SE = 9.41) at the lower elevation site, respectively, in 2013. Average reproductive plant density was 70.0 individuals/100 m<sup>2</sup> (SE = 8.71) at the higher elevation site and 66.8 individuals/100 m<sup>2</sup> (SE = 8.02) at the lower elevation site in 2016. We found clear differences in *Croton* reproductive plant density between years ( $51.3 \pm 3$  SE plants in 2013 and  $73.6 \pm 7$  in 2016) but did not find clear differences between sites (Table 1).

Average monthly soil temperature between September 2018 and March 2019 was  $30.44 \pm 0.01^\circ\text{C}$  at the lower elevation site and  $25.93 \pm 0.01$  at the higher elevation site (Figure 1). Monthly average of soil water content was  $0.093 \pm 0.0002$  m<sup>3</sup>/m<sup>3</sup> at the lower elevation site and  $0.136 \pm 0.0002$  m<sup>3</sup>/m<sup>3</sup> at the higher elevation site. Soil water content loss after a rain was faster at the lower elevation site (Figure 1, right plot).

### 3.1 | Femaleness of *Croton* as a function of plant size and conspecific neighborhoods

The two most likely models for femaleness ( $G_i$ ) variation of *Croton* included (a) site and sum of canopies of five closest neighbors, and (b) site, plant size, and plot-level density as predictors (see Table S2). Femaleness at the lower elevation site was greater than at the higher elevation site (coefficient =  $0.29 \pm SE 0.0481$ ; Table 2). A positive relationship was found between femaleness and plant size (volume log transformed) of *Croton* in the two sites; femaleness increased

**FIGURE 1** Monthly average temperature (left) and monthly average of water content (right) in soil in winter season from September 2018 to March 2019 at the higher elevation site (1,700 a.s.l.) and at the lower elevation site (1,400 a.s.l.)



**TABLE 2** Effects of site, plant size (log volume cm<sup>3</sup>), and density on femaleness of *Croton* evaluated with a linear mixed-effects models fit by REML

Fixed effects	Value	SE	df	t-Value	p-Value
Site at 1,700 m (reference)	0.2989	0.0481	998	6.2213	.0000
Site at 1,400 m	0.0380	0.0076	143	4.9957	.0000
Plant size	0.0127	0.0036	143	3.5477	.0005
Density	0.0001	0.0002	143	0.7804	.4365

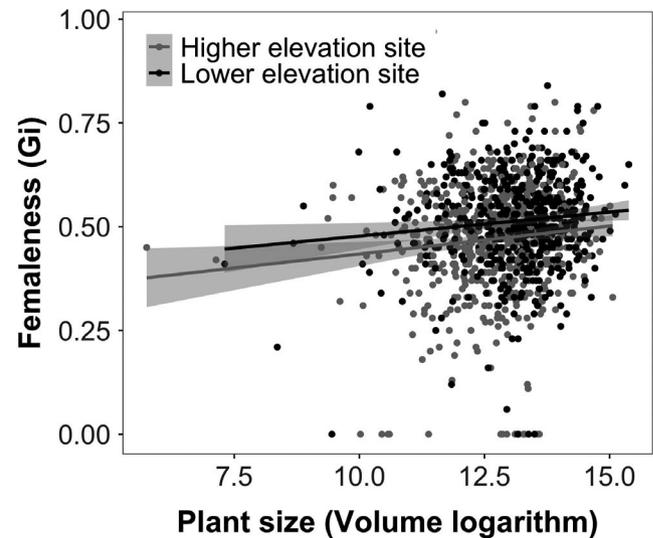
Abbreviations: *df*, degrees of freedom; *SE*, standard error.

as plant size increased, that is, per unit increase in plant size there was an average of 0.01 increase in femaleness ( $0.012 \pm SE = 0.0036$ ; Table 2, Figure 2). There was an interaction between the effect of site and that of canopy area of the five closest neighbors on femaleness. We observed that the canopy area of the five closest neighbors had a positive effect on *Croton* femaleness at the low elevation site, but this effect disappeared at the high elevation site (Table 3, Figure 3; Table S2).

### 3.2 | Spatial patterns of femaleness between years and sites

The results of Ripley's K-function in 2013 at the higher elevation site (1,700 a.s.l.) indicated a uniform spatial pattern of femaleness of *Croton* in two plots in ranges between 0–0.5 m and 0.5–1 m (Figure 4). In the other plots, femaleness had a random pattern (see Table S1). At the lower elevation site (1,400 a.s.l.), femaleness had an aggregated spatial pattern on a plot in ranges between 0.5–1 m and 1–2.5 m (Figure 4). In the other plots, femaleness had a random pattern (see Table S1).

In 2016 at the higher elevation site femaleness of *Croton* showed uniformity in a plot in a range between 0.5–1 m and aggregation in a plot in range between 1–1.5 m (Figure 4). The other plots showed a random pattern of femaleness (see Table S1). At



**FIGURE 2** Scatterplot showing the relationship between femaleness (*Gi*) and plant size (volume logarithm) of *Croton* at the higher elevation site (1,700 a.s.l.) and at the lower elevation site (1,400 a.s.l.)

the lower elevation site, femaleness showed an aggregated spatial pattern on a plot in ranges between 0–0.5 m and 1–2.5 m (Figure 4). The other plots showed a random pattern of femaleness (see Table S1).

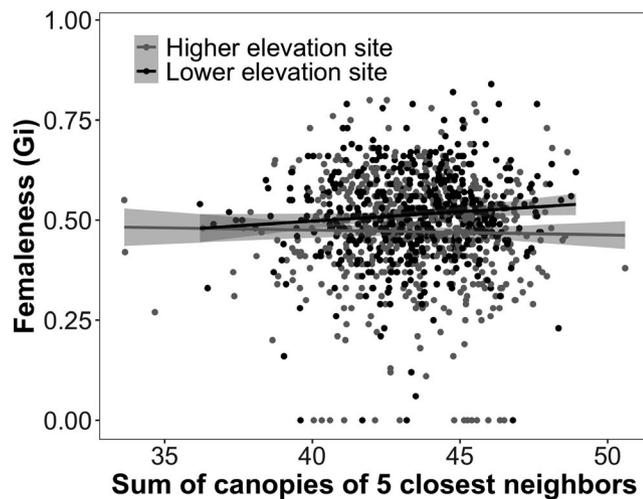
### 3.3 | Evaluation of spatial patterns of femaleness between sites

We did not find clear grouping or repulsion differences between sites in 2013 (BTSS = 2,527.95,  $p = .26$ , Figure 5a) nor in 2016 (BTSS = 1,026.06,  $p = .47$ , Figure 5b). By contrast, comparing the averaged K-functions between 2013 and 2016, clear differences were found between years for both at the higher elevation site (Wilcoxon signed-rank test  $V = 5$ ,  $p < .0001$ ) and at the lower elevation site (Wilcoxon signed-rank test  $V = 93$ ,  $p < .0001$ ).

Fixed effects	Value	SE	df	t-Value	p-Value
Site at 1,400 m (reference)	0.3099	0.1114	998	2.7810	.0055
Site at 1,700 m	0.2176	0.1479	143	1.4709	.1435
Sum of canopies of five closest neighbors	0.0047	0.0027	143	1.8299	.0693
Site at 1,400 m × sum of canopies of five closest neighbors	-0.0060	0.0034	143	-1.7619	.0802

**TABLE 3** Effect of interaction between site and sum of canopies of the five closest neighbors on femaleness of *Croton* evaluated with linear mixed-effects models fit by REML

Abbreviations: *df*, degrees of freedom; *SE*, standard error.



**FIGURE 3** Scatterplot showing the relationship between femaleness (*Gi*) and sum of canopies (Canopy logarithm) of *Croton* at the higher elevation site (1,700 a.s.l.) and at the lower elevation site (1,400 a.s.l.)

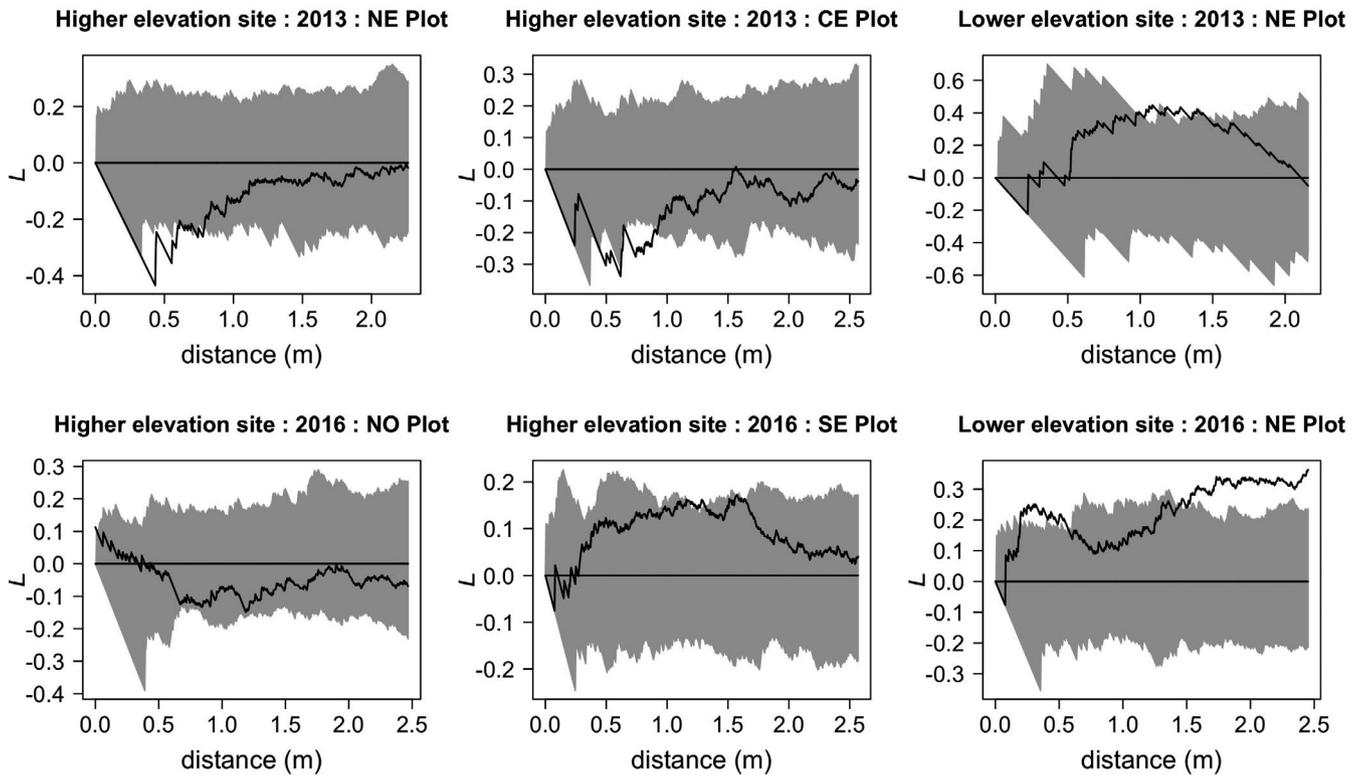
## 4 | DISCUSSION

### 4.1 | Site, plant size, and canopies of conspecific neighbors of *Croton*

Our results indicated higher femaleness in *Croton* at the lower elevation site, located at 1,400 a.s.l., than at the higher elevation site, located at 1,700 a.s.l. Because our study lacked replication for elevation the effects of this variable were confounded with those of the sites and any interpretation of these data on the consequences of elevation on femaleness of *Croton* should be considered as tentative pending its corroboration in future studies. Lower elevation was associated with a greater presence of female individuals in *Juniperus communis* subsp. *alpina* in the Sierra Nevada in southeastern Spain (Ortiz, Arista, & Talavera, 2002; from 2,100 to 2,700 a.s.l.), *Taxus baccata* in the Marche region, central Italy (Garbarino, Weisberg, Bagnara, & Urbinati, 2015; from 450 to 770 a.s.l.), and *Valeriana edulis* in the Rocky Mountains of Colorado, USA (Petry, Soule, Iler, et al., 2016; from 2000 to 3,790 a.s.l.). We also found that larger plants had greater femaleness in both sites studied. In tropical mountain ecosystems, there is greater availability of nutrients at lower elevations (Homeier, Breckle, Günter, Rollenbeck, &

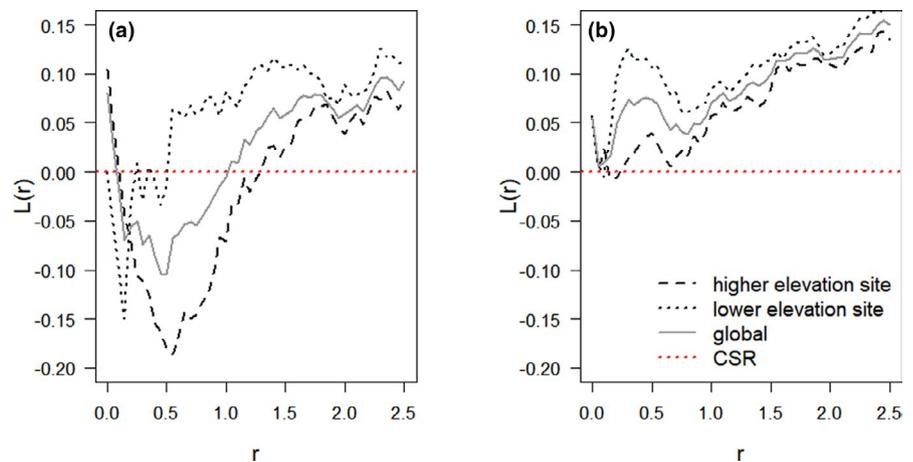
Leuschner, 2010; Soethe, Wilcke, Homeier, Lehmann, & Engels, 2008). Increase of nutrients at lower elevations could contribute to higher growth and investment of resources to femaleness in *Croton* (Calviño, & Galetto, 2010; Klinkhamer, de Jong, & Metz, 1997). In monoecious species, this relationship has been less studied possibly because it may be more practical to evaluate spatial segregation of clearly female individuals into dioecious species (Aizen, & Kenigsten, 1990; Bleher, Oberrath, & Böhning-Gaese, 2002).

Conspecific neighboring canopy area influenced *Croton's* femaleness. Similar results were found in *Croton* at the same elevations when evaluating the effect of conspecific density but over total flower production (male flowers and female flowers) in *Croton* (Lara-Romero, Gusmán-M, Ramón, Vélez-Mora, & Espinosa, 2017). Although there was no clear difference in density between sites, influence of canopies of conspecific neighbors was positive at the lower elevation site favoring femaleness in *Croton*. Shrub canopy can improve microenvironmental conditions, accumulation of organic matter, nutrients in soil (Moro, Pugnaire, Haase, & Puigdefábregas, 1997), and improve water availability (Holmgren, Scheffer, & Huston, 1997; Sagar, Pandey, & Singh, 2012) making the climatic conditions at the lower elevation site (high temperatures and low water content) more favorable for growth and expression of femaleness in *Croton* (Butterfield, Bradford, Armas, Prieto, & Pugnaire, 2016; Holmgren, Scheffer, & Huston, 1997; Lara-Romero et al. 2016; Lara-Romero, Gusmán-M, Ramón, Vélez-Mora, & Espinosa, 2017; Pugnaire, & Luque 2001). *Croton* is a dominant shrub and constitutes a nurse species that contributes to regulate the functioning of the dry inter-Andean shrubland community (Espinosa, Luzuriaga, de la Cruz, & Escudero, 2014). Absolute conspecific density should be considered in subsequent work since a positive relationship between *Croton* density and femaleness could improve supply of water and nutrients to invest in reproductive functions. Although negative effects due to density-dependent mortality caused by seed predation and fungal attack would also have to be assessed (Cascante, Quesada, Lobo, & Fuchs, 2002; Fujimori, Samejima, Kenta, et al., 2006). The heterospecific density of this species also could influence its own femaleness. Similarly, in alpine plant communities from Europe, North and South America, Asia, and a sub-Antarctic island it was found that greater richness among the facilitating species increased the reproductive performance of the nurse species (Schöb, Michalet, Cavieres, et al., 2014).



**FIGURE 4** Spatial distribution of femaleness in *Croton* study plots. Patterns of femaleness of *Croton* in 2013 (top) and in 2016 (bottom) determined by Ripley's K-Function (estimated L) at the higher elevation site (1,700 a.s.l.) and at the lower elevation site (1,400 a.s.l.). NE, NO, SE and CE mean plots northeast, northwest, southeast, southwest, and center, respectively, regarding the larger plot. The gray area represents the confidence envelope that limits the area determining the random pattern; the continuous lines above the envelope represent the aggregated spatial pattern and, below, the uniform pattern of femaleness of *Croton* in the plots studied. Note that y-axes show different scales for clarity. Plots that had a defined spatial pattern are shown

**FIGURE 5** Averaged  $K(r)$  functions for each of the sites (transformed as  $L(r) = \sqrt{K(r)/\pi} - r$  to facilitate interpretation). CSR: expected value of complete spatial randomness. Global: overall average  $K(r)$  function. Left panel corresponds to 2013 and right panel to 2016



## 4.2 | Spatial patterns of femaleness in *Croton*

Aggregation of *Croton* femaleness was observed in some plots at the lower elevation site (1,400 a.s.l.). A study developed in a tropical forest in Panama where past and current spatial patterns of a community of 298 different species of shrubs, understory, mid-canopy, and top-canopy trees were explored suggested that the monoecious reproductive system could also be a variable associated with the aggregation of species (Flügge, Olhede, & Murrell, 2012). The spatial

patterns found at the lower elevation site supports the hypothesis that the expression of femaleness in monoecious species could be favored by conspecific facilitation processes (Garbarino, Weisberg, Bagnara, & Urbinati, 2015; Ortiz, Arista, & Talavera, 2002; Soliveres, Maestre, Berdugo, & Allan, 2015). Uniform or random spatial patterns of femaleness in *Croton* found in other plots could be due to changes in survival that affect density between years causing conspecific interactions to change direction and become negative or neutral (Bruno, Stachowicz, & Bertness, 2003; Ludwig, Dawson, Prins, Berendse, & de Kroon, 2004; Tielbörger, & Kadmon, 2000). It

is possible that if we had performed a spatial survey from a grid as suggested by Wiegand, Kissling, Cipriotti, & Aguiar (2006), we would have had more possibilities of finding spatial patterns in the remaining plots considering size and especially shape of each plant.

Spatial analysis of *Croton* in a previous study revealed that aggregation was greater at high altitude and inhibition at short scales (<1 m; Ramón et al. 2016). Increased grazing at high altitudes and higher rainfall contrasts between elevations with climate change can favor larger differences in *Croton*'s survival between altitudes and consequently increase differences in density between their populations (Anderegg, Anderegg, Sherman, & Karp, 2012; Bai, Ma, Zhang, Su, & Leng, 2019; Gilfedder, & Kirkpatrick, 1994; Jonasson, Medrano, & Flexas, 1997). This may indicate that the benefits of positive interactions may be more contrasting between elevations.

## 5 | CONCLUSIONS AND LIMITATIONS

Our study shows how factors such as site, plant size, and neighborhood canopies can influence the expression of femaleness and the generation of spatial aggregation of femaleness in a monoecious shrub of an inter-Andean dry scrub. We present evidence that the expression of femaleness in monoecious species can be influenced by the same factors that influence the spatial segregation of female individuals in dioecious species. We point out that spatial patterns found at the lower elevation site, where higher soil temperatures and lower moisture content occurred, support the hypothesis that femaleness in monoecious species can be favored by interactions of conspecific facilitation. We also highlight the importance of continually evaluating hetero- and conspecific interactions to ensure the persistence of *Croton* in the dry inter-Andean scrubland in southern Ecuador.

We focus on the early part of *Croton* flowering season and additional work will be necessary to complete the description of the spatial distribution of femaleness of this species. Our fieldwork was carried out between November–December in 2013 and 2016. When we began this work, there was no information available on flowering behavior of our focal species. Later, in 2017–2019, we documented its flowering phenology and observed that flowers were available during a longer interval (September to April; Figure S3). We also observed that the variation in beginning and in extent of *Croton* flowering depended on the schedule and intensity of rains with earlier starts in some years. As with many researchers, the timing and frequency of our field activity are strongly constrained by budgets and academic schedules. During 2013 and 2016, we were able to find plenty of flowers allowing us to characterize femaleness during the study interval. However, future studies should be implemented to assess the whole flowering annual season.

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## CONFLICT OF INTEREST

The authors have no conflict of interest.

## AUTHOR CONTRIBUTIONS

Vélez-Mora involved in conceptualization, project administration, data collection and curation, analysis, funding acquisition, supervision, writing and editing. Ramón involved in analysis, writing and editing. Vallejo involved in data collection and curation, writing and editing. Romero involved in data collection and curation, writing and editing. Duncan involved in conceptualization, writing and editing. Quintana-Ascencio involved in supervision, analysis, methodology, writing and editing.

## DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x69p8czfx> (Vélez-Mora et al. 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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