Can debarking affect the sex ratio, population structure and spatial segregation? Insights of unsustainable harvesting in a Mesoamerican tropical tree

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ABSTRACT

The ecological mechanisms that contribute to maintaining plant populations have been exhaustively examined worldwide, but the relative quantification of the effects of anthropogenic processes on these mechanisms in tropical dioecious tree species has not yet been performed. The aim of this study was to analyze the effects of debarking on the sex ratio, population structure, distribution and spatial correlation between the sexes and growth stages of *Amphipterygium adstringens* (Anaciardiaceae), a dioecious tree species that is highly exploited for its medicinal bark. We found differences in plant density between the harvested and nonharvested stands. The sex ratio was 1.33♂:1♀in the harvested stands, while the opposite was true for the nonharvested stands (1.27♀:1♂), which suggested that selective debarking drives androic skewing and has an impact on reproductive performance. However, despite the dominance of a certain sex in terms of relative frequency under each condition, we did not observe spatial sex segregation since the analysis suggested that the spatial independence pattern did not differ between sites. In contrast, facilitation requirements (spatial attraction) between androic plants and plants and between seedlings and saplings were found in nonharvested areas, while spatial uniformity patterns at the population level suggest strategies to avoid competition over space and finite resources in stressful environments. These novel findings indicate that debarking not only modifies the spatial and population structure of a Mesoamerican tropical tree but also influences the sex ratio, consequently affecting the long-term conservation of *A. adstringens* stands.

Keywords: Sex ratio, cuachalalate, medicinal bark, population structure, Ripley's K function, spatial pattern, seasonally dry tropical forests.

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SIGNIFICANCE STATEMENT

Spatial sex segregation in woody dioecious species from seasonally dry tropical forests worldwide has rarely been studied, and even less is known about when there is an anthropic component that could affect intra- and interplant population interactions. *Amphipterygium adstringens* (Anacardiaceae), a tropical dioecious tree highly exploited for its medicinal bark, is selectively harvested, and gynoic trees are preferred over androic ones. This induces populations with higher proportions of androic plants in commercially harvested areas, which may reduce their reproductive performance. We strongly believe that this original contribution strengthens our understanding of the ecology and management of Mesoamerican tropical trees because (1) this study is the first to analyze the effects of forest exploitation on the sex ratio of dioecious plants and the consequences for the performance of the populations and (2) it provides novel information for the spatial sex segregation theory, taking as a model a dioecious species under harvest.

INTRODUCTION

Sex *sensu stricto* is a concept linked to genetic origin (specific selection to sex) from the cromosomic differentiation of individuals to sexual function (Bonduriansky 2007; Rhen 2007). Dimorphism in dioecious plants is defined as the sex-by-gender expression of both ginoecious or female (♀) and androecious or male (♂) phenotypes.

Dioecious plants may exhibit traits from a sex-dependent life history (Delph 1999), especially when gynoecious organisms allocate a larger proportion of resources for reproduction and a smaller proportion for maintenance and growth than do androecious organisms (Barret and Hough 2013; Munné-Bosch 2015). Differences in reproductive costs between the sexes arise because the resources required to produce seeds and nectar generally exceed those for pollen grain production (Lloyd and Weber 1977; Pyke 1991; Geber et al. 1999; Pacini and Nepi 2007).

Spatial segregation of the sexes is defined as a reduction in the likelihood that male and female gametes in dioecious populations will encounter each other if the average distance between sexes increases (Lloyd and Weber 1977). This scenario may decrease the average reproductive success of each of the sexes by limiting the dispersal distance of the pollen (Bierzychudek and Eckhart 1988). Overall, this process drives the structural conformation of stands, where a common spatial pattern is the randomness of trees of different sexes, which generally occurs by natural selection because of landscape heterogeneity (Freeman et al. 1976; Dale and Fortin 2014; Szmyt 2014).

At the local scale, spatial segregation of the sexes is often associated with an environmental gradient of limited resources, such as available soil moisture (Bierzychudek and Eckhart 1988; Dawson and Ehleringer 1993; Dudley and Galen 2007; Field et al. 2013a), nutrients (Cox 1981; Bierzychudek and Eckhart 1988), elevation (Ortiz et al. 2002; Kang and Shin 2012; Field et al. 2013a), rainfall (Verdú and García-Fayos 1998; Álvarez-Cansino et al. 2013),

salinity (Bram and Quinn 2000) and solar radiation (Nicotra 1998; Nuñez et al. 2008; Álvarez-Cansino et al. 2013). Therefore, spatial segregation of the sexes is linked to differential reproductive costs in dioecious plants and may reflect differences in the resources needed for growth, reproduction and survival in different habitats (Bierzychudek and Eckhart 1988; Queenborough et al. 2007; Barret and Hough 2013). This can affect the long-term reproductive success and persistence of dioecious plant populations (Field et al. 2013a).

Spatial segregation of the sexes in dioecious woody species of seasonally dry tropical forests has been poorly studied by ecologists, in contrast with the findings for tree species of tropical rainforest (Queenborough et al. 2007; Sinclair et al. 2012; Barret and Hough 2013; Munné-Bosch 2015), in which the study of the effect of biotic interactions on organisms' spatial patterns has even been deepened (Réjou-Méchain et al. 2011; Newton et al. 2012; Vedel-Sørensen et al. 2013; van Lent et al. 2014). Additionally, for this scientific area, there is a lack of information about the effect of human activities such as sex-selective tree debarking on plant population consequences.

For example, differences in phenology between male and female plants can temporarily bias the sex ratio. There are cases of nonbiased sex ratios (1:1) in tropical trees as well. Gynoecious plants may be underrepresented in a population if flowering and reproduction are delayed (Queenborough et al. 2007; Forero-Montaña et al. 2010) or if they bloom less frequently than androecious plants (Sinclair et al. 2012; Field et al. 2013a). Hence, the sex ratio of dioecious tree species in tropical rainforests generally represents the majority of androecious plants (♂>♀) rather than a balanced ratio (1♂:1♀) (Sinclair et al. 2012; Barret and Hough 2013; Field et al. 2013b; Munné-Bosch 2015). Species with gynoecious predominance have been reported for only the genus *Garcinia* (Clusiaceae) in Asia and in the Paleotropical rainforest region (Thomas 1997), as well as for two species of the Polygonaceae family, *Coccoloba caracasana* Meisn. and *Triplaris americana* L. (Opler and Bawa 1978)

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and for different members of the Sapindales order (Opler and Bawa 1978; Forero-Montaña et al. 2010) from the Neotropical region (Caribbean islands and central Mexico to southern South America).

The exploitation of nontimber forest products (NTFPs) is another factor that synergizes with environmental variables and increases pressure on dioecious plants since it leads to changes in their spatial and population structure and dynamics (Hernández-Barrios et al. 2012; Jansen et al. 2018; Ticktin et al. 2012; van Lent et al. 2014; Varghese et al. 2015; Baldauf et al. 2021). Quesada et al. (2011) showed that dioecious tree species in Mesoamerican seasonally dry tropical forests are the most vulnerable to habitat fragmentation since this process has a negative impact on the reproductive biology and pollination syndromes of woody plants. Despite the importance of tropical dry forests as a supply source for various NTFPs globally (Djoudi et al. 2015), we have limited understanding of the ecological response of harvested dioecious plants in terms of spatial segregation of the sexes, populations and spatial structure and spatial correlation between parental sexes, seedlings and saplings (Romero-Manzanares et al. 2016). Even less is known about tree species threatened by an excessive demand for vital functional structures such as bark (Gaoue and Ticktin 2007; Baldauf and dos Santos 2014; Romero 2014; da Silva et al., 2018; Beltrán-Rodríguez et al. 2020, 2021, 2022ab; Baldauf et al. 2021).

Particularly, for Mesoamerican seasonally dry tropical forests, the research was carried out with *Amphipterygium adstringens* (Schltdl.) Standl. (cuachalalate) stands out. It is a dioecious and endemic tree whose medicinal bark is considered the most important NTFP in Mexico (Beltrán-Rodríguez et al. 2020, 2021). However, given its intensive harvest and high international demand, *A. adstringens* is classified as the most vulnerable medicinal plant in Mexico (Beltrán-Rodríguez et al. 2017). In addition, the overexploitation of *A. adstringens* is increasing because the bark of gynoecious plants is in high demand because of its better quality; therefore, its collection rates are greater than those of androecious plants (Beltrán-Rodríguez et al. 2020). This scenario is further enhanced by considering that gynoecious trees have a higher postdebarking mortality rate (Beltrán-Rodríguez et al. 2021).

Traditional management of *A. adstringens* is a rudimentary process limited to three debarking techniques aimed mainly at trees with reddish inner bark (gynoiecious) (Beltrán-Rodríguez et al. 2020, 2021, 2022a), in which a curved machete is used to either (i) cut down standing individuals, (ii) debark 100% of the shaft and the branches, or (iii) partially debark 50% of the trunk. The first two techniques are

destructive and cause individual death, while in the third case, the wounds heal in a two- to four-year period according to the harvesters (Hersch-Martínez 1999; Rodríguez 2003). Experimental debarking has shown that the use of *A. adstringens* is sustainable if less than 50% of the shaft of gynoecious trees with a diameter at breast height >20 cm is harvested during the rainy season (Beltrán Rodríguez et al. 2021).

According to our expertise, the spatial segregation of the sexes has not been analyzed in seasonally dry tropical forests; moreover, studies have focused less on dioecious species subject to expoliative harvesting because bark is valued as a medicinal resource and where one of the sexes is preferred by users. With these pronouncements, we assumed that the spatial segregation of the sexes was multifactorial.

In this study, we investigated the effects of debarking on the sex ratio, population structure, spatial correlation, and distribution between the sexes and the growth stages of *A. adstringens*. The purpose of this study was to gain further insights into how the exploitation of a Mesoamerican tropical dioecious tree drives ecological processes related to dispersion, habitat occupancy and spatial interaction between individuals. On the other hand, this research contributes to the spatial segregation of the sexes theory.

We hypothesized that selective debarking and overharvesting of *A. adstringens* will induce damage to reproductive performance or mortality in gynoecious stands with an androecious-skewed sex ratio. Since the reproductive performance of both sexes may be affected, there may be an impact on the population and spatial structure of *A. adstringens*. We also hypothesize that harvested stands will exhibit population structure with null reproduction and poor recruitment at all growth stages, while nonharvested populations will exhibit an inverted j-shaped distribution—right skewness—(such as the plethora of seasonally dry tropical trees; Ruiz et al. 2005; Coelho et al. 2017; Lanuza et al. 2023), implying differences in the density of growth categories. Additionally, we expect spatial independence and randomness between the different growth stages (seedlings, saplings and adults) to prevent competition for space and finite resources in stressful environments.

MATERIAL AND METHODS

Study area

The study took place in the central-southern region of Mexico in the Sierra de Huautla Biosphere Reserve (REBIOSH) (18°33'17.3"-18°29'5.4" N and 98°57'43.2"-98°54'10.1" O). This area is one of the main regions where *A. adstringens* was commercially harvested in Mexico. The region comprises different

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altitudinal intervals (650 m to 1790 m) and has a warm subhumid climate [Aw0" (w) (i') g], the driest of which are subhumid climates (García 2004). It has a mean annual temperature of 22.7°C (min 22–max 34°C) and a mean annual rainfall of 863 mm, 90% of which is registered between May and October. The region's dominant vegetation type is seasonally dry tropical forests consisting mainly of secondary forest fragments at different stages of ecological succession (Beltrán-Rodríguez et al. 2018).

Study species

Amphipterygium adstringens (SLtdl.) Standl. (Anacardiaceae) is a deciduous, dioecious and polycarpic tree (Cuevas, 2005) locally known as "cuachalalate". It is endemic to Mexico, and its distribution is restricted to hillsides and ravines in seasonally dry tropical forests, where it is one of the dominant species (Beltrán-Rodríguez et al. 2018). *Amphipterygium adstringens* populations are generally dense ($\sim$ 470 trees ha^{-1} considering different growth stages and sexes) and exhibit an aggregated distribution pattern (Ortega-Baranda et al. 2023; Ramos-Ordoñez et al. 2022). In addition to its ecological importance, *A. adstringens* has long been used in Mexico (with some registers being at least 500 years old; Hernández 1959) and is considered one of the most socioculturally and economically important NTFPs in the country (Beltrán and Bye 2023). The species' bark is commercialized for the treatment of 25 different illnesses, and it is exported to the USA and Europe for its anticarcinogenic, antigastric, astringent and hypocholesterolemic properties (Oviedo-Chávez et al. 2004; Sotelo-Barrera et al. 2022). Since their reddish bark is associated with increased efficacy resulting from the concentration of active compounds, female trees are subject to debarking (Navarrete and Mata 2009).

Sampling design

The study area in the REBIOSH was subjected to rainfed agriculture 49 years ago, and the slash and burn system was used to open clearings in seasonally dry tropical forests; as a result, the landscape has fragmented vegetation (Beltrán-Rodríguez et al. 2018). One section of this area (16 ha) has not been harvested for the last 30 years by community agreements to avoid their exploitation, so it represents a local conservation territory where *A. adstringens* plants are not harvested. Another section of the study area (29 ha) is represented by open access areas that are harvested to obtain medicinal and food products, firewood and wood for local construction; among these areas, the debarking of 50% of the *A. adstringens*

trunk is one of the most common activities (Beltrán-Rodríguez et al. 2018).

We established eight 30 × 30 m permanent plots to sample the populations of *A. adstringens*, and we separated them according to harvesting conditions: four in the harvested stands and four in the nonharvested stands. To determine the "pool" of plots with and without harvest in the study area, participatory mapping (Stockdale and López-Binnqüist 2019) was applied with collectors (n=39) of *A. adstringens* bark. From the total sample of plots (n=56) represented in the landscape, we randomly selected eight plots placed in secondary seasonally dry tropical forest areas (45 ha), with a minimum equidistance of 7.0 km between each plot.

The environmental factors recorded in each plot were altitude, relative air humidity, mean annual temperature, total rainfall, slope and solar radiation. The altitude was measured with a global geopositioning system (GPS MAP 62SC, Garmin, Mexico). The relative air humidity, mean annual temperature and total rainfall were obtained from the "Sierra de Huautla" weather station (AWSSH) for the nonharvested plots and from the "El Limon" weather station (17057; CSEL) for the harvested plots (Servicio Meteorologico Nacional 2010). The slope (%) was measured with a clinometer (Kode KB-14/360, Suunto, USA). Solar radiation was calculated with the algorithm proposed by Oke (1987) based on slope and azimuth. The azimuth is the angle generated between the north reference point and the plot, measured with a compass.

Field assessment

Population structure and sexes

All the *A. adstringens* plants within each plot were tagged and classified by growth stage. *Amphipterygium adstringens* plants were categorized as follows: seedlings 1, seedlings 2, saplings 1, saplings 2, adults 1, adults 2 and adults 3 (Table 1). The seedling and sapling (nonreproductive individuals) diameter corresponds to the basal diameter, whereas the adult (reproductive trees) diameter refers to the diameter at breast height (1.30 m). The sex of each reproductive tree (adult) was determined by the observation of floral structures (presence of an androecium or gynoecium) or fruits (gynoecious *vs.* androecious trees) and, in the absence of these structures, especially in the vegetative phenological stage, by bark color. A gynoecious tree was identified by a red bark color, whereas a white color was considered to indicate an androecious tree (Beltrán-Rodríguez et al. 2022ab).

Table 1. Size categories used to classify *Amphipterygium adstringens* plants according to height and diameter. The seedling and sapling (nonreproductive individuals) diameter corresponds to the basal diameter, whereas the adult (reproductive trees) diameter refers to the diameter at breast height. Adults were identified by sex. The data were obtained from four sites per harvesting condition (H= harvested, NH= not harvested).

Growth stages	Height(cm)	Diameter (cm)	Harvesting condition	Number of individuals*
Seedlings 1	0-10	0.1-0.5	H	0
			NH	10
Seedlings 2	10-20	0.5-1	H	0
			NH	8
Saplings 1	20.1-100	1.1-2.5	H	0
			NH	25
Saplings 2	100.1-500	2.6-5	H	0
			NH	1
Adults 1	500.1-700	5.1-15	H	46
			NH	42
Adults 2	700.1-1000	15.1-25	H	60
			NH	29
Adults 3	>1000	≥ 25.1	H	8
			NH	2

Legend: *N=231 individuals. Only adults: H=114 (49 ♀, 65 ♂), NH= 73 (39 ♀, 34 ♂).

Spatial distribution

The criterion used to analyze the distribution pattern consisted of recording the total number of individuals for each growing stage (seedlings, saplings, adults by sex) to establish spatial interactions. The spatial location of each *A. adstringens* plant was determined in the field through Cartesian distances (m), using the bottom left corner of each plot, with the slope as the origin point (0, 0). This procedure was carried out as a complementary way to visualize the observed spatial pattern (Dale and Fortin 2014) of *A. adstringens* individuals by plot and condition, considering both all the plants and the interactions between them.

Data analysis

Environmental variables

To determine whether there were significant differences in the environmental variables between the harvested and nonharvested sites and, consequently, to exclude the possible influence of their effects on dispersal and spatial correlation patterns, we performed a Mann–Whitney U test for independent samples.

The analyses were developed using R (R Development Core Team 2023).

Population structure

We compared the size distributions of the harvested and nonharvested stands using skewness (S_x^3) and kurtosis (S_x^4) coefficients and evaluated the influence of debarking (represented as present or absent) on the population structure of *A. adstringens* through a χ^2 test (Vásquez-Cortez et al. 2020). To test the size class distribution, the bell-shaped curve represented a normal distribution and was considered the reference model. In contrast, skewness ($S_x^3= 0$) represents a symmetrical distribution, and kurtosis ($S_x^4= 0$) displays a mesokurtic distribution. A skewness greater than or less than zero represents the degree of asymmetry in the size class distribution. If > 0, the distribution is positive and right skewed; if $S_x^3 < 0$, the distribution is negative and left skewed. Kurtosis describes the shape of the size class distribution, and a kurtosis greater than or less than zero represents changes in the shape of the normal curve. If $S_x^4 < 0$, the distribution is leptokurtic, and the shape of the distribution curve is high and thin; if $S_x^4 < 0$, the distribution is platykurtic, and the shape of the curve is

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width and flat (Infante-Gil and Zárate de Lara 2010).

Sex ratio

For statistical purposes, the sex ratio of *A. adstringens* was calculated following the numerical relationship between sexes with asymmetric proportions and binomial distributions versus the use of the sex ratio sensu stricto (1 androecious:1 gynoecious; Wilson and Hardy 2002). These authors emphasized that the sex ratio nonsu sensu stricto is based on the following equation: (number of androecious plants/number of androecious plants + number of gynoecious plants), which leads to fewer statistical errors than does the sex ratio sensu stricto. Therefore, we tested for significant differences in the sex ratio estimated sensu stricto (based on the equation mentioned) between harvested and nonharvested stands, assuming that harvested stands contained harvested trees and that the unharvested stands contained only trees not debarked. A χ^2 test was carried out. All analyses were performed in R (R Development Core Team 2023).

Univariate distribution pattern of populations harvested vs nonharvested

The spatial distributions of the harvested and nonharvested *A. adstringens* trees were analyzed per sex in adults and between adults and plants at other growth stages. Graphical comparisons between harvested and nonharvested stands were obtained using the univariate Ripley's $K(t)$ function (Ripley 1977). This function describes the evolution of the $K(t)$ function with distance (t) for each plot and, in general, through the coordinates (x, y) of all the individuals in different growth stages. The $\lambda K(t)$ (λ = intensity) function is defined as the expected number of plants within the distance t of an arbitrary plant. $K(t)$ is defined as:

$$K(t) = n^{-2} A \sum \sum_{i=j}^{-1} W_{ij}^{-1} I_t^{(u_{ij})}$$

where n is the number of individuals in plot A; $|A|$ is the area of the plot; u_{ij} is the distance between the ith and the jth individuals in A; $I_t(u) = 1$ if $u \leq t$ and 0 if not; and W_{ij} is the fraction of the circumference of a circle centered at the ith individual with radius uij that lies inside A.

$K(\mathrm{t})$ is calculated through the sum of all the pairs of individuals no greater than t (Ripley 1977; Diggle 1983). This result is transformed through a square root to simplify its interpretation (Besag 1977):

$$L(t) = \sqrt{\frac{K(t)}{\pi}} - t$$

where $K(t)$ is Ripley's function, π is 3.1416, and t is the distance. Finally, we established the confidence intervals of the Poisson-type distribution of the $L(t)$ function through 999 Monte Carlo simulations (Besag and Diggle 1977).

The decision criteria for the distribution pattern are defined by $L(t)$: a value of $L(t) = 0$ implies that the spatial pattern with radius t is random; values of $L(t) > 0$ reflect clumping, while values of $L(t) < 0$ suggest a uniform distribution. The null hypothesis of this analysis is spatial randomness. Therefore, if the values of $L(t)$ are outside the confidence limit, the null hypothesis is rejected. A line above the confidence limit indicates a significant spatial clumping pattern, whereas a line below the confidence limit indicates a uniform spatial pattern.

Bivariate correlation pattern to spatial associations

The spatial correlation patterns between the sexes (gynoecious and androecious plants) and between the sexes and growth stages (seedlings and saplings) of *A. adstringens* were analyzed with the bivariate $L_{12}(t)$ function obtained from the transformation of Ripley's $K_{12}(t)$ function:

$$K_{12}(t) = (n_1 n_2)^{-1} A \sum_{i=l}^{n_1} \sum_{i=j}^{n_2} W_{ij}^{-1} I_t^{(u_{ij})}$$

(Ripley 1977; Lotwick and Silverman 1982). The interpretation of this function is simplified by linearizing as $L_{12}(t)$ (Szmyt 2014; Velázquez et al. 2016).

The null hypothesis of the bivariate analysis is spatial independence. A value of $L_{12}(t) = 0$ indicates that both groups are spatially independent (graphically, this spatial pattern is represented by a line between the envelopes); $L_{12}(t) > 0$ reflects spatial attraction (graphically, it is shown by a line that touches or exceeds the envelope at its upper limit), while $L_{12}(t) < 0$ expresses spatial repulsion (graphically, it is shown by a line that touches or exceeds the envelope at its lower limit). The significance (P $\leq$ 0.01) of the $L_{12}(t)$ function was determined using Monte Carlo simulations (Besag and Diggle 1977; Szmyt 2014), and its upper and lower limits were defined with 99% confidence. Univariate and bivariate patterns were generated with Ripley software (Fisher 2000).

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RESULTS

Environment and harvesting conditions

The environmental variables analyzed (altitude, relative air humidity, mean annual temperature, total rainfall, slope and solar radiation) were significantly similar between the harvested and nonharvested areas (Table 2).

Population structure between stands

We registered a total of 117 plants in the nonharvested stands: 18 seedlings, 26 saplings, and 73 adults differentiated into 39 gynoecious and 34 androecious plants. Populations of harvested stands are represented exclusively per adult individual, 49 gynoecious and 65 androecious (Table 3).

The frequency of *A. adstringens* individuals at all growth stages was different between the harvested and nonharvested stands ($\chi^2 = 58.5$, df = 6, P < 0.0001). The population structure between stands confirmed this approach since the adult plant density in nonharvested areas was greater than that in nonharvested areas, and no seedlings or saplings were registered in harvested stands. Similarly, the populations in both conditions presented negative asymmetry ($S_{NH}^3 = -0.404$ and $S_H^3 = -0.786$) and leptokurtic size class distributions ($S_{NH}^4 = 1.362$ and $S_H^4 = 1.576$; Figure 1a, b).

Sex ratio in harvested and nonharvested stands

The sex ratio was also significantly different between the harvested and nonharvested stands ($\chi^2 = 30.6$, $df = 7, P < 0.000007$). The ratio of gynoecious plants was greater in nonharvested stands (1.27 ♀: 0.78 ♂), while the ratio was skewed toward androecious plants in harvested stands (0.75 ♀: 1.33 ♂) (Figure 2).

Univariate distribution pattern of populations harvested vs nonharvested

Under both harvesting conditions, the univariate spatial distribution exhibited a combination of the three different spatial patterns (Figure 3b). In the nonharvested stands, spatial randomness and aggregation were the dominant patterns (Figure 3c-d), except for one plot with a completely uniform organization ($L(t) < 0$; Figure 3a). In contrast, all the plots in the harvested stands exhibited a random and uniform pattern (Figure 3e-h), with a weak trend toward aggregation at small distances in only two cases (Figure 3g-h), which suggested that debarking affects the spatial structure of *A. adstringens*.

Bivariate correlation pattern to spatial associations

According to our bivariate analysis, there were no differences in spatial organization between androecious and gynoecious plants due to debarking, given that both nonharvested (Figure 4a-d) and harvested (Figure 4e-h) plants maintained spatial independence patterns ($L_{12}(t) = 0$).

These findings were consistent with the finding that -$L_{12}(t) = 0$- and that there was a significant correlation between gynoecious plants and both seedlings (Figure 5a-d) and saplings (Figure 5e-h). Conversely, the spatial relationships between androecious plants and seedlings (Figure 6a-d) and saplings (Figure 6e-h) and between seedlings and saplings (Figure 7a-h) exhibited weak but significant spatial attraction patterns at short (0–2.8 m), medium (5.8–9.7 m) and large (12.1–13.2 m) distances. According to the results of the Mann–Whitney U test, environmental variables did not explain (P > 0.01) the observed differences between the spatial patterns of harvested and nonharvested sites (Table 1).

DISCUSSION

The null effects of the environmental variables on the ecological parameters of A. adstringens.

The environmental variables analyzed among the harvested and nonharvested areas (altitude, climate elements, slope and solar radiation) were statistically similar according to the Mann–Whitney U test. The advantage of environmental similarity between the two conditions is that the responses observed in the plants of the different stands are produced by other conditions not estimated, such as human intervention and activities carried out at the site. Therefore, we can assure that the physical environment is homogeneous and has no effect on the dispersal and spatial correlation patterns of *A. adstringens* populations.

Trends in the population structure of *A. adstringens* stands.

The population structure based on stem diameter exhibited an asymmetric left-skewness distribution because there were no seedlings or saplings in the harvested stands, while in the nonharvested stands, there were plants in the first four categories, although the density was low. A similar population structure was described for *Picrasma javanica* Blume and *Erythroxylum kunthianum* Kurz, which are two tropical dioecious trees from northeastern India that have been historically harvested (Laloo et al. 2006),

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Table 2. Mann–Whitney U test for environmental variables in harvested (H) *vs.* not-harvested (NH) stands of *Amphipterygium adstringens*. Mean ± SD of four sites per harvesting condition.

Environmental variables	Harvesting condition	Mean ± SD	*P value*	*W*
Altitude (m)	H	1163 ± 26.8	0.999	18
	NH	1165.7 ± 29.6		
Relative air humidity (%)	H	31.3 ± 14.0	0.228	13.5
	NH	30.9 ± 13.7		
Mean annual temperature (°C)	H	24.6 ± 2.7	0.228	22.5
	NH	24.9 ± 1.1		
Total rainfall (mm)	H	795.2 ± 199.6	0.386	26
	NH	742.9 ± 183.4		
Slope (%)	H	27.2 ± 1.7	0.857	19
	NH	26.7 ± 2.2		
Solar radiation (W/m^2)	H	277.7 ± 369.1	0.114	24
	NH	256.3 ± 354.1		

Table 3. Number of individuals (N) per harvesting condition in the stands.

Growth stages	Harvested (H)	Non harvested (NH)
Seedlings 1	0	10
Seedlings 2	0	8
Saplings 1	0	25
Saplings 2	0	1
Adults 1	46	42
Adults 2	60	29
Adults 3	8	2
⌐ N=231 individuals Only adult trees	H=114114 (49 ♀, 65 ♂)	NH=11773 (39 ♀, 34 ♂)

but in contrast with the higher density of seedlings and saplings of other tropical species associated with their fecundity and capacity for regeneration (Freckleton et al. 2003). In the *A. adstringens* case, the asymmetry registered under both conditions is partially consistent with the hypothesis for the harvested stands, with the exception that our findings demonstrate the tolerance of trees with larger DBH in this condition, almost 60% of which are androecious trees and therefore not as valued by harvesters.

For the nonharvested stands, a population structure with an inverted j-shaped distribution (right skewness) was expected due to the lack of human intervention. However, our findings show that asymmetry to the left is not an exclusive output of the harvesting effect; if so (due to the effect of the population status before the establishment of the exclusion), it is more likely that the duration of no human intervention in the stands (49 years) has had an influence. Natural regeneration in these stands is favored by the absence of extensive livestock farming, the use of timber and nontimber forest products and induced forest fires, which allows the few seedlings that have been successfully established to survive and transition to other growth stages without being browsed, trampled or burnt by external agents (Beltrán-Rodríguez et al. 2018). This confirms that anthropic absence has allowed the recovery of old impacted stands, mean-
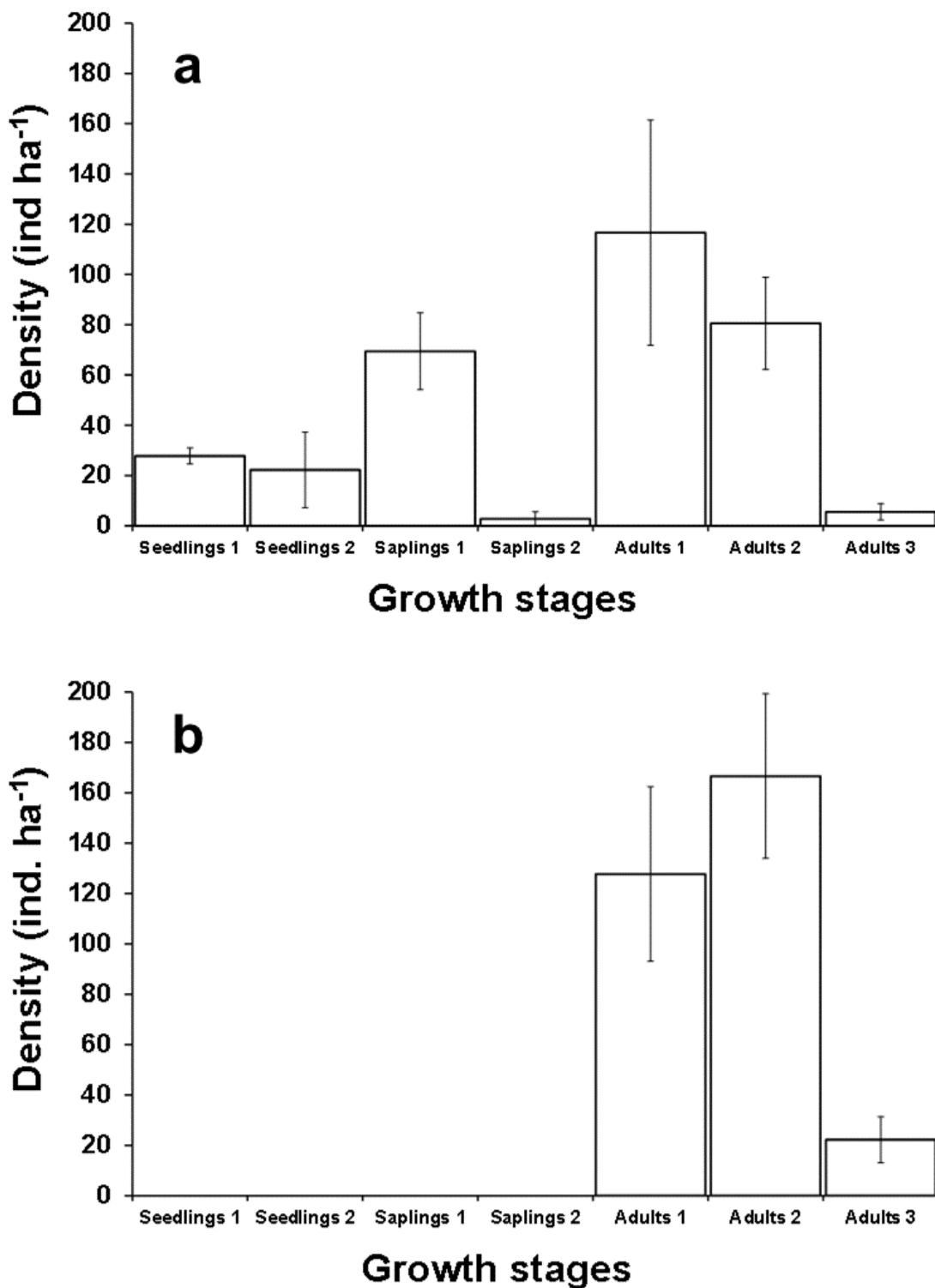
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Figure 1. Population structure of *Amphipterygium adstringens* in nonharvested (a) and harvested (b) stands. The lines on each bar represent the standard error estimated.

ing that exclusion has been the practice management that has sponsored the survival and growth of the first growth stages in nonharvested stands (Beltrán-

Rodríguez et al. 2021, 2022a).

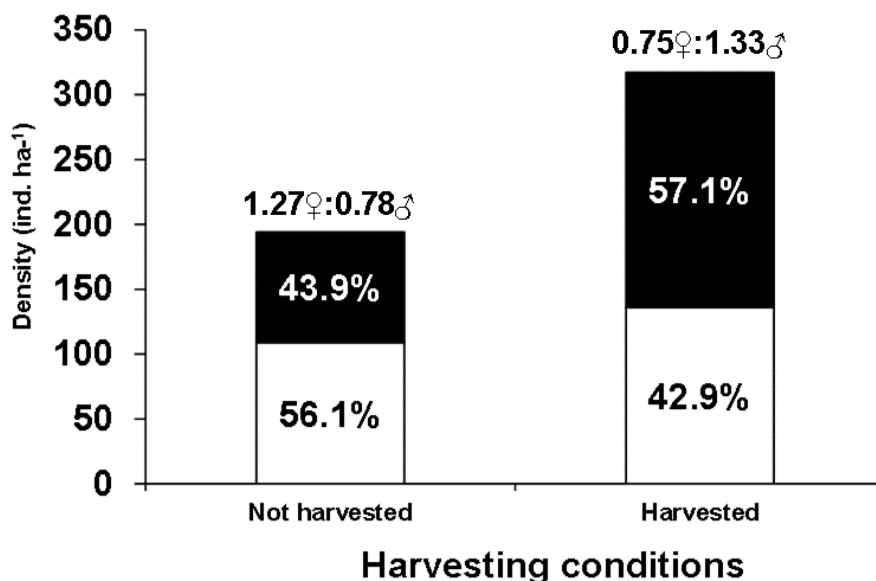The left-skewed distribution of *A. adstringens* (predominance of tree categories with larger diame-

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Figure 2. Population density and sex ratio of *Amphipterygium adstringens* in nonharvested *vs.* harvested stands. The ratio of gynoecious trees is presented in white, and the ratio of androecious plants is presented in black.

ters in nonharvested stands) differs from that in previous research (Botha et al. 2004; Gaoue and Ticktin 2007). These authors reported a right-skewed distribution (where the mean plant diameters predominate in the smaller categories while the larger ones are absent) for *Catha edulis* Forssk., *Rapanea melanophloeos* (L.) Mez and *Khaya senegalensis* (Desr.) A. Juss., which are tropical dioecious trees from Africa whose bark is also commercialized as an NTFP. In these cases, debarking affects the categories of trees with larger stem sizes. A similar pattern was observed for tropical dioecious African trees, such as *Anogeissus leiocarpa* (DC.) Guill. & Perr. (Schumman et al. 2011), *Garcinia mannii* Oliv. (Roland et al. 2013) and *Cola nitida* (Vent.) Schott and Endl. (Savi et al. 2018), which are commercially debarked and right skewed.

According to *A. adstringens*, we would anticipate that if the species persists in exclusion as it is currently (t0), due to stand regeneration, it is likely that over time (t+1...n), it tends to normalize the population structure. In contrast, at harvested sites, it would be advisable to temporarily isolate the area from human activities to start recovering the affected populations, especially in small size categories. Because they are the most vulnerable to other disturbance factors and not to debarking, the bark, which is the object of harvesting, has not yet developed during these growth stages.

The sex ratio as an expression of the impact of bark harvest

Considering all the growth stages, the highest population density of *A. adstringens* was detected in non-harvested areas (325 *vs.* 317 plants ha^{-1}). The difference between the two densities according to condition was nonsignificant, but it is worth highlighting that all the plants in the harvested stands were reproductive plants (Table 3). Therefore, debarking *A. adstringens* has a negative impact on the relative frequencies of the greatest size categories, but this does not seem to affect the total density of mature plants in the harvested stands. According to recent studies, bark regeneration in *A. adstringens* is greater on gynoecious trees than on androecious trees (Beltrán-Rodríguez et al. 2021). This finding might be attributed to the high capacity for bark regeneration and plant survival after debarking ($< 85\%$ mortality, N= 72 trees), which constitutes a possible resilience strategy for *A. adstringens* populations in stressful environments and is also displayed by other debarked species worldwide (Romero 2014).

The absence of seedlings and saplings on harvested stands indicates reproductive problems for the species (Freckleton et al. 2003). Given the similar environmental conditions between stands (Table 1), we could attribute this phenomenon to the synergistic effect of the decrease in reproductive gynoecy (Figure 2),
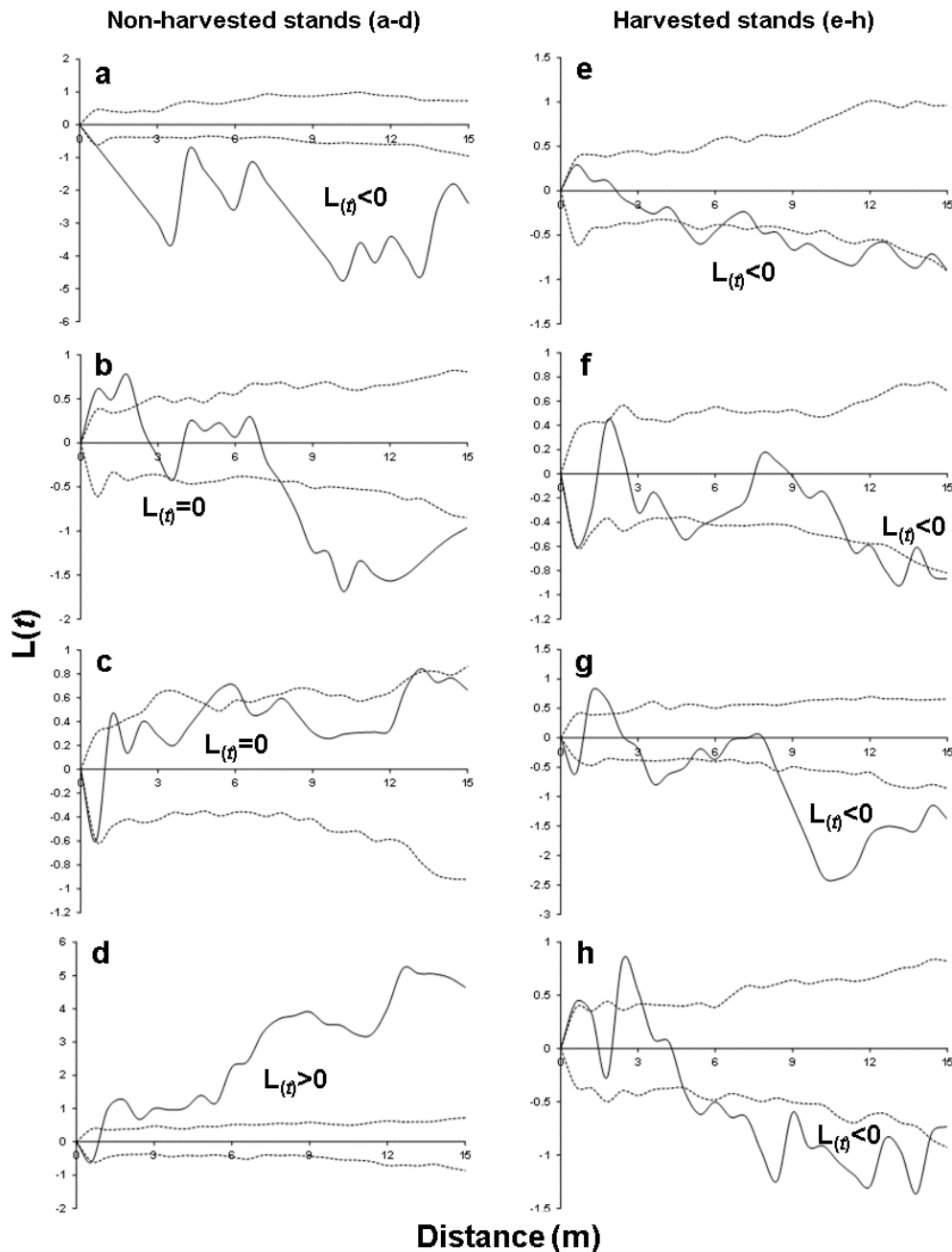
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Figure 3. Univariate spatial analysis of all growth stages of *Amphipterygium adstringens* by plot in non-harvested and harvested stands. The dotted lines correspond to the upper and lower limits of the confidence interval ($\alpha = 99\%$). The solid line is the distance between spatial point patterns.

the genetic problems associated with seed production and empty seeds (López-Zariñana 2017) and the negative impact of other anthropogenic disturbances on vital rates (Beltrán-Rodríguez et al. 2022a). These findings support the proposed hypothesis (Ho = harvested populations will show asymmetry in population structure) since the selective debarking of gynoecious trees within harvested sites affects reproductive performance, an apparently common pattern in other tropical NTFPs (da Silva et al. 2018), but which, in our case, manifests over time in androecious-skewed plant populations.

Notably, in the nonharvested area, bark conservation (or lack of poor harvest management) allows gynoecious trees to prevail over the density of male trees. This result is consistent with the findings of
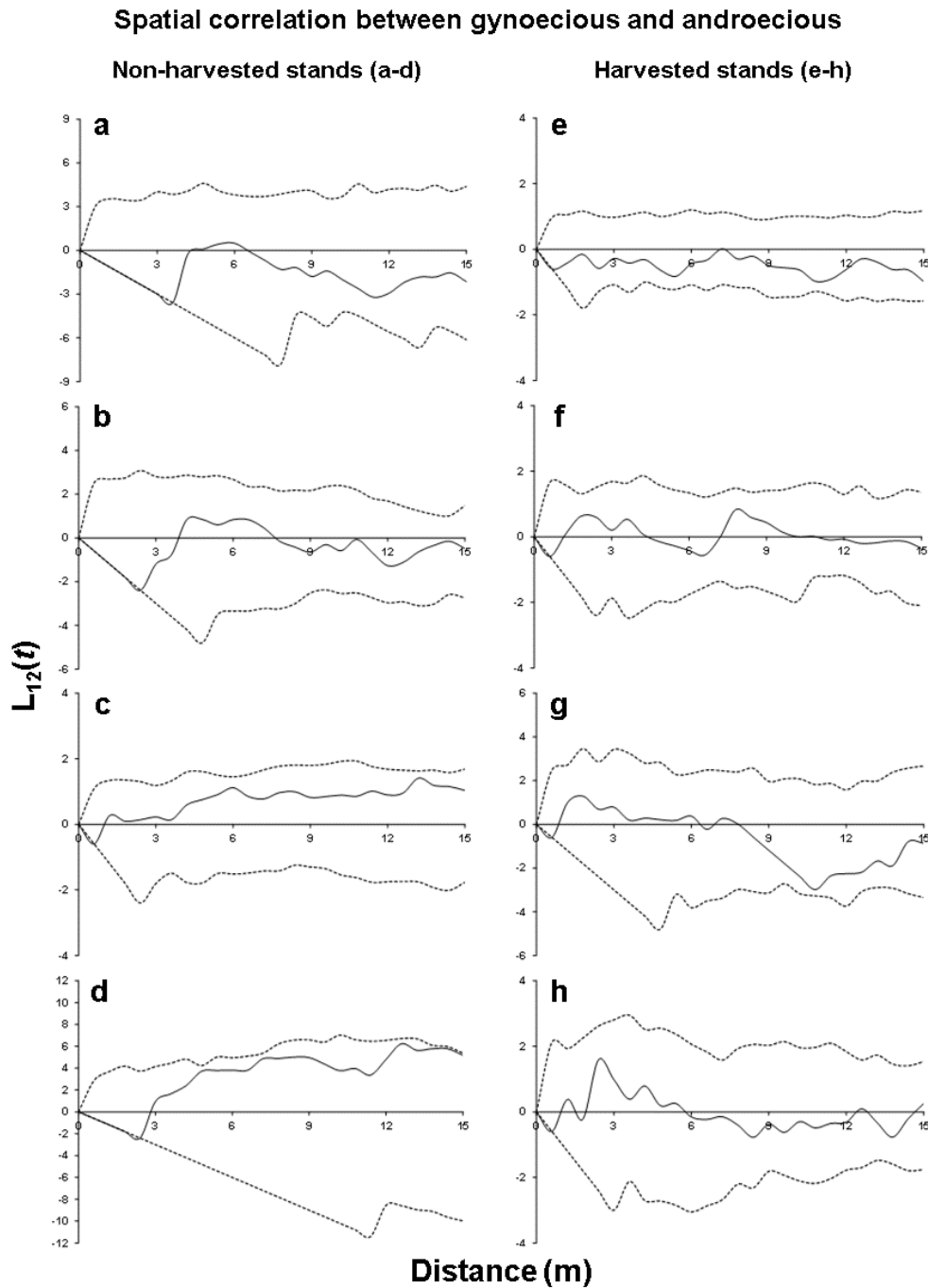
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Figure 4. Spatial correlation analysis between gynoecious and androecious *Amphipterygium adstringens* plants by plot in nonharvested and harvested stands. The dotted lines correspond to the upper and lower limits of the confidence interval ($\alpha = 99\%$). The solid line is the distance between spatial point patterns. All the charts show $L_{12}(t) = 0$.

multiple studies in other tropical forests around the world, given that the sex ratio in highly stressful environments tends to be androecious-skewed (Bierzychudek and Eckhart 1988; Queenborough et al. 2007; Barret and Hough 2013). However, our study is the first published study to date to date to show that the sex ratio of a tropical dioecious tree can be affected by more than just environmental factors.

We highlight that these novel findings do not contradict some of the theoretical evidence showing that gynoecious plants have greater mortality than androecious plants (Nicotra 1998; Delph 1999). In
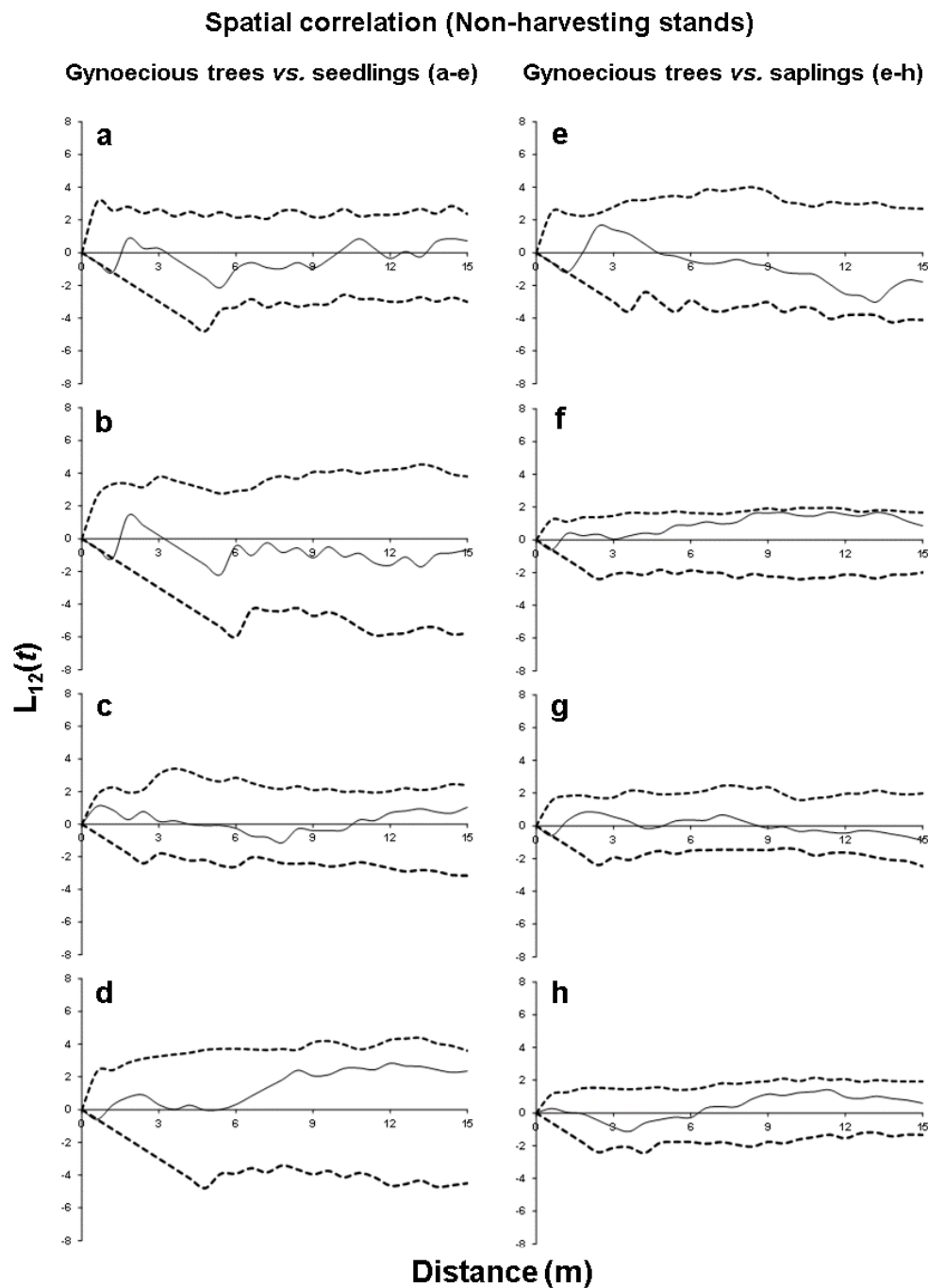
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Spatial correlation (Non-harvesting stands)

Gynoecious trees *vs.* seedlings (a-e)   **Gynoecious trees *vs.* saplings (e-h)**

Figure 5. Spatial correlation between gynoecious trees and seedlings (a, b, c, d) and between saplings (e, f, g, h) of *Amphipterygium adstringens* and nonharvested stands. The dotted lines correspond to the upper and lower limits of the confidence interval ($\alpha = 99\%$). The solid line is the distance between spatial point patterns.

our case, this difference in performance is explained by the lower postdebarking survival rate (60%, N= 10) in this sex (Beltrán-Rodríguez et al. 2021) than by the increase in energy allocated for reproduction *vs.* other vegetative functions (resource allocation at higher growth rates or sizes), which is generally ex-
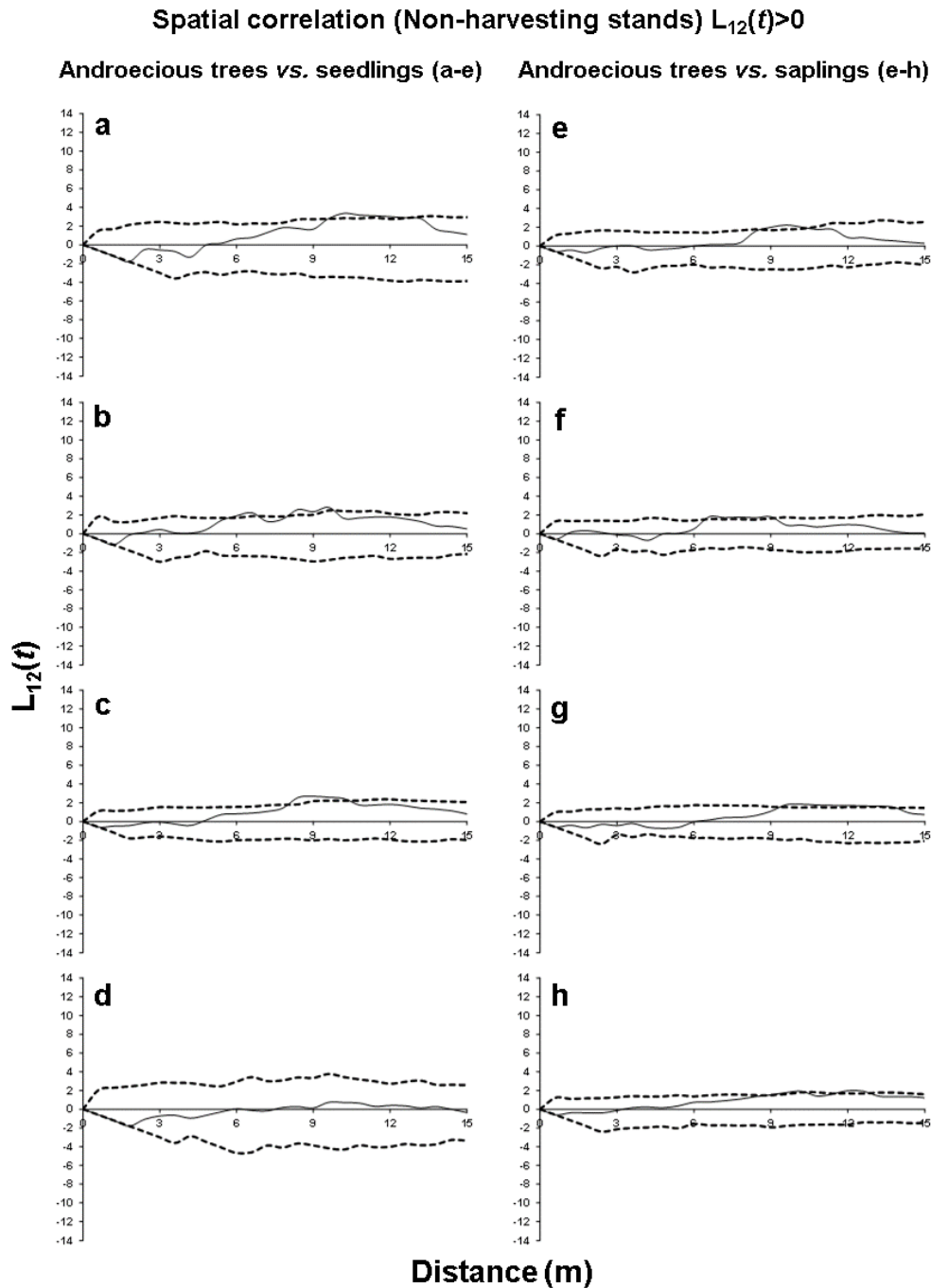
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Figure 6. Spatial correlation between androecious trees and seedlings (a, b, c, d) and between saplings (e, f, g, h) of *Amphipterygium adstringens* and nonharvested stands. The dotted lines correspond to the upper and lower limits of the confidence interval ($\alpha = 99\%$). The solid line is the distance between spatial point patterns.

hibited by gynoecious plants (Lloyd and Webb 1977; Bierzychudek and Eckhart 1988; Dawson and Geber 1999; Geber et al. 1999; Obeso 2002; Sinclair et al. 2012; Barret and Hough 2013).

In fact, gynoecious *A. adstringens* plants present structures associated with a higher level of conduc-

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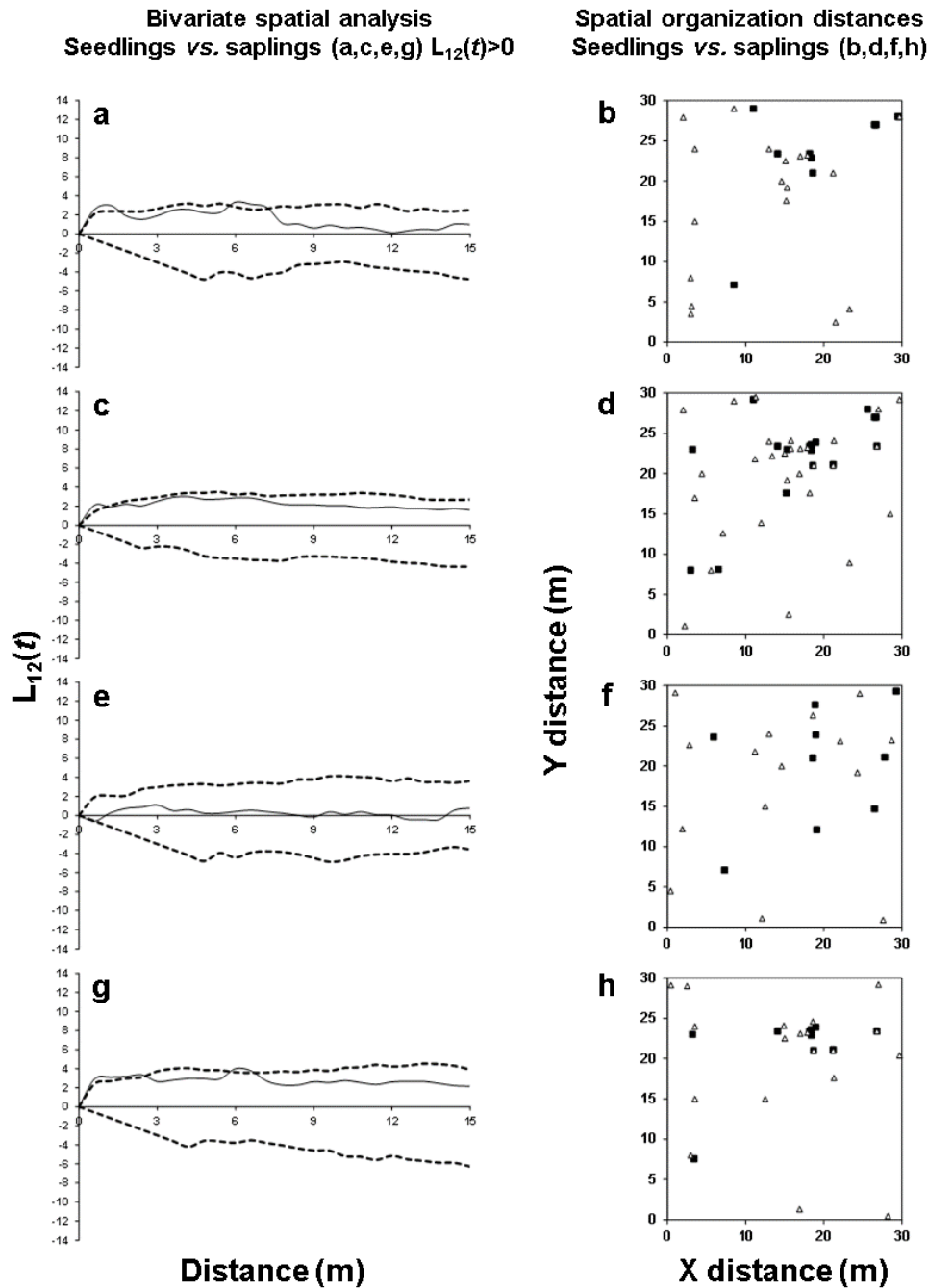
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Figure 7. Bivariate spatial analysis between *Amphipterygium adstringens* seedlings and saplings in nonharvested stands (a, c, e, g). The dotted lines correspond to the upper and lower limits of the confidence interval ($\alpha = 99\%$). The solid line is the distance between spatial point patterns. Spatial organization distances between seedlings (black squares) and saplings (white triangles) by plot (b, d, f, h).

tivity and hydraulic safety in their secondary xylem, which endows them with a greater radial growth rate than does androecious plants (Beltrán-Rodríguez 2018; Beltrán-Rodríguez et al. 2022b). Even though greater growth leads to less efficient water use be-

cause of high evaporative demand through stomatic conduct (Dawson and Geber 1999; Pittermann 2010), it also allows trees to reach the superior canopy faster and increase their competitive capacity, ensuring reproduction (Poorter et al. 2009; Wright et al. 2010;

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Zanne and Falster 2010).

Consequently, it is possible that there is a trade-off between radial growth and reproduction to compensate for mortality induced by selective debarking in gynoecious *A. adstringens* plants. Overall, we believe that the high energetic cost of massive fruit production (Luna-Nieves et al. 2017; Hidalgo-Contreras 2019) associated with tree hydraulic efficiency and size maximization (Beltrán-Rodríguez, 2018) is compensated for by a reduction in female inflorescence and flower dimensions, as well as a smaller average number of flowers (Cuevas 2005) and viable seeds per fruit (López-Zariñana 2023). Similar results have been reported for other dioecious long-lived woody species (Obeso 2002; Barret and Hough 2013).

Therefore, in agreement with Delph (1999) and Mckown et al. (2017), we suggest that the life history of each sex of *A. adstringens* may be a consequence of both differential patterns in resource allocation in response to specific eco-physiological needs due to their reproductive strategies (Niklas 1997; Obeso 2002) and a response to selective pressures induced by debarking (Baldauf and dos Santos 2014; Romero 2014; da Silva et al. 2018). Overall, these synergistic effects favor certain vital rates (Beltrán Rodríguez et al. 2022a) and could contribute to a specialized occupation of the growth space (Zanne and Falster 2010; Field et al. 2013a).

Debarking does not drive spatial sex segregation

Despite our evidence of the dominance of a certain sex in each condition (harvested *vs.* nonharvested; Figure 2), we did not observe spatial segregation of the sexes. This finding contrasts with the theory (Bierzychudek and Eckhart 1988; Barret and Hough 2013) since debarking induces physiological stress at the individual level (Baldauf and dos Santos 2014; Romero 2014) and environmental stress when trees are cut down and forest gaps appear (Beltrán-Rodríguez 2018). Therefore, we would have expected the dominance of androecious plants in the richest spaces in terms of resources (Cox 1981; Munné-Bosch 2015). In contrast, the bivariate analysis reflected a spatial independence pattern between the sexes for *A. adstringens*.

On the one hand, these results seem to indicate that debarking does not direct a negative spatial interaction (habitat segregation) between androecious and gynoecious *A. adstringens* plants. These findings agree with observations of other tropical dioecious trees and shrubs without nontimber exploitation (Nicotra 1998; Forero-Montaña et al. 2010; Queenborough et al. 2007). However, as Réjou-Méchain et al. (2011) noted for other tropical dioecious species from Cameroon and Central Africa, this could be caused by the underrepresentation of specific habitats associated with each sex due to the scale of the analysis and the environmental homogeneity between the compared conditions, as in the present study (Table 1). Research conducted with other NTFPs of the *Copaifera* spp. genus in the Brazilian Amazon region confirms these suppositions since spatial patterns may vary intraspecifically or interspecifically if analyzed at a local or a landscape scale (Newton et al. 2012). Future studies that include spatial variation within the analysis are necessary to confirm the supposed absence of spatial segregation of the sexes in *A. adstringens* since the repetitions per plot under each condition currently do not display environmental variability.

Debarking drives spatial interactions between parental trees and other growth stages

Regarding the bivariate distribution between parental sex and growth *stage*, we partially rejected our hypothesis given that we found a spatial attraction pattern only at different distances between androecious plants and both seedlings and saplings and between seedlings and saplings. These positive interaction patterns could suggest facilitation mechanisms to compensate for extreme drought and direct light conditions typical of tropical deciduous forests for seasonally dry tropical forests, especially during the dry season (Vieira and Scariot 2006; Quesada et al. 2011). In fact, *A. adstringens* plants are semi-tolerant to shade (Rincón and Huante 1993), which indirectly explains the spatial pattern that we found. Finally, because plants need to associate with other shrub species and with adults of small crowns to ensure their survival under their canopy, *A. adstringens* seedlings require a nurse plant. However, multiple studies have also shown that climate seasonality and phenological variation in seasonally dry tropical forests induce changes in intra- and interspecific interaction mechanisms, switching from facilitation to competition and vice versa (Vieira and Scariot 2006; McDonald et al. 2010; Méndez-Toribio et al. 2014). This could also explain the differences in the spatial correlations between the sexes of *A. adstringens* and the different growth stages.

The spatial independence between gynoecious plants and both seedlings and saplings would imply a strategy to avoid competition and mortality in early stages. In the present study, this could be explained by the constant radial growth rate and foliar biomass production of the gynoecious *A. adstringens* trees, which resulted in the development of larger individuals with more extensive canopies (Beltrán-

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Rodríguez 2018). These allometric conditions could affect the microclimate of the understory and, consequently, the establishment and growth of seedlings and saplings. This situation could become even more accentuated since more than 80% of indehiscent fruits have an average maximum dispersal distance of 5 m (Hidalgo-Contreras 2019). This probably explains why none of the fruits (N=1,080) that were experimentally placed under the mother tree canopy produced seeds that germinated within a year (López-Zariñana 2023). This finding suggested that only fruits that are dispersed longer distances (up to 15 m) are able to establish themselves and survive under the crown of other species or of androecious *A. adstringens* trees since their canopies are less dense and allow optimal amounts of sunlight to filter through.

However, even though there tends to be a stronger association between different growth stages and androecious plants, the spatial distribution of plants in nonharvested stands follows an aggregated pattern that has been attributed to limited dispersion in other tropical dioecious species (Muller-Landau and Hardesty 2005; Seidler and Plotkin 2006). In contrast, although *A. adstringens* debarking does not affect the spatial correlation between the sexes, it does influence the spatial distribution at the population level because it promotes the maximization of the distance between neighboring plants (spatial uniformity; Szmyt 2014). Although uniform dispersal was observed in all the plots of the harvested *A. adstringens* stands, it was also registered in some of the nonharvested stands (Figure 3a-b), which suggests that the equidistant gradual mortality associated with this pattern's ecological explanation (Hubbell 1979; Condit et al. 2000) could be independent of the management conditions (harvested *vs.* nonharvested) for *A. adstringens*.

For nonharvested stands, this result is supported by the previous explanation of the bivariate test between gynoecious plants and both seedlings and saplings, where density dependence between these size categories could lead to mortality at early stages, inducing a uniform pattern in reproductive trees, which are numerically more abundant. In contrast, in the case of harvested stands, the complete absence of these growth stages (seedlings and saplings) as well as the lower total density compared to those of nonharvested stands could explain the spatial uniformity (Condit et al. 2000; Dale and Fortin 2014).

CONCLUSION

The topics previously discussed represent the theoretical basis for an alternative design of conservation strategies and sustainable use of a tropical dioecious species with medicinal importance, which was not referred to in previous worldwide analyses. This research is particularly important because it represents one of the first numerical evaluation efforts in the silviculture of NTFPs from Mesoamerican seasonally dry tropical forests useful for its bark.

Although the data generated in this study did not originate from an experimental design, the scenario evidenced by our results suggest (if the current trends and rate of debarking continue) that a negative impact on the mid- and long-term reproductive performance, natural regeneration and intra- and interspecific biotic interactions of *A. adstringens* populations. Since harvest tends to be selective for gynoecious plants, it also affects the sex ratio without generating spatial sex segregation.

These novel results highlight the need to consider the sexual condition of a plant when designing sustainable silvicultural practices for other dioecious NTFPs. Additionally, these findings provide evidence that harvesting can drive forest dynamics in tropical dry ecosystems because it modifies the spatial interaction of plants.

To achieve conservation of *A. adstringens* stands, some silvicultural practices were mentioned in this paper. However, multiple criteria should be considered, such as bark harvest of both sexes, enrichment practices in harvested areas to favor the presence of seedlings and saplings, and an assisted nursery system that provides better conditions for the growth of these nonreproductive plants.

ACKNOWLEDGMENT

DATA AVAILABILITY

The data used to support the findings of this study are available from the corresponding author upon reasonable request.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

CONTRIBUTION STATEMENT

Conceived of the presented idea: LBR, ARM LBR and AMB carried out the experiment.
LBR, ARM, TT, JB, and OG carried out the data analysis.
Wrote the first draft of the manuscript: LBR, ARM.
Reviewed and performed the final write-up: LBR, ARM, TT, AMB, JB, OG, RB
Supervised the work: ARM, RB.

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