



Fencing promotes fast recovery of demographic processes after grazing-driven collapse in *Bursera graveolens* forests

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ABSTRACT

Global change pressures are jeopardizing the functioning and structure of most tropical forests and clouding the future for their biodiversity and provided services. Although the impact of direct destruction through deforestation and fragmentation is currently in the research portfolio, overgrazing, which is more diffuse and generalized but chronic, especially in the seasonal dry forests, has been by far less addressed. Overgrazing can lead to a dramatic change in natural regeneration, often triggering the collapse of dominant species.

The almost monospecific dry forests of *Bursera graveolens*, one of the most representative forest of the Tumbesian region, are on the verge of extinction due to both direct destruction and chronic overgrazing and regeneration collapse in forest remnants. Here, we evaluated the impact of a very simple measure, the installation of fences, on the regeneration of ecological processes affecting the dominant species. We mapped and measured all *Bursera* individuals with a height greater than or equal to 30 cm in six 1-ha plots, 3 within and 3 outside fenced areas. Using spatial point pattern analysis, we inferred the importance of demographic and ecological processes affecting adults and juveniles in fenced and unfenced areas.

The spatial structure of adults was similar in fenced and unfenced areas, varying from random to aggregated patterns, showing that fences did not interfere with ecological processes affecting adult trees. On the contrary, we found 2765 juveniles in the three fenced plots but none in free ranging areas. Juveniles showed heterogeneous clustered patterns, and their distribution and growth were negatively influenced both by the presence and the height of adult trees. On average, there was an exclusion zone of 10 m around adult trees where recruitment of juveniles was limited. Competition among juveniles appeared to be negligible.

All in all, these results suggest that, in addition to recruitment, two of the main mechanisms that rule tree population dynamics in tropical forests, i.e., dispersal limitation and a Janzen-Connell-like mechanism favoring recruiting far from adult trees have been immediately restored in the fenced area. This shows that fencing is a viable tool for a fast regeneration and conservation of *Bursera* forests.

1. Introduction

Deforestation and fragmentation are among the main drivers of global change, contributing to the rapid loss of tropical forests with important implications for ecosystem functioning and biodiversity conservation (Tapia-Armijos et al., 2015). This is part of a complex degradation process in which deforested areas and forest remnants are lately subjected to other drivers of global change in a cascade process.

Overgrazing is probably one of the most widespread and pervasive impacts suffered by forest remnants and, since it hinders regeneration of dominant tree species, it is considered an important threat for dry tropical forests (Aguirre and Kvist, 2005).

Although livestock grazing can induce different impacts on the abundance of plant populations, both positive and negative (Adler et al., 2001), by limiting the recruitment of seedlings (Janzen, 1988), it often generates even-aged stands where trees could reach senescence at the

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same time (Meiners et al., 2015). This net effect depends on the herbivore foraging strategy, its density and, also, on how the dominant plant species resists herbivory (Augustine and McNaughton, 1998). The regeneration collapse and subsequent forest dieback result in a loss of biodiversity and ecosystem services.

Unfortunately, evidence points to very intense negative effects of overgrazing in seasonally dry tropical forests, with dramatic changes in the composition and structure of the community that also leave profound and detectable spatial signals in the structure of the different life stages of dominant tree species (Augustine and McNaughton, 1998; Cipriotti and Aguiar, 2005; Clark and Clark, 1981; Stern et al., 2002) and even, in many cases, suppressing regeneration at all (Janzen, 1988; Milchunas and Lauenroth, 1993; Stern et al., 2002; Hamann, 2004). Livestock grazing is a strong modifier of vegetation across the Tropics (Bernardi et al., 2019). It modifies the incidence of (natural) herbivory (Norghauer et al., 2014; Norghauer and Newbery, 2016; Norghauer et al., 2016) and alters vegetation structure by influencing the demographic processes of coexisting plant populations (Adler et al., 2001; Cipriotti and Aguiar, 2005) including the recruitment of dominant tree species (Adler et al., 2001). It is a well-known fact that the spatial pattern of dispersed seeds determines the subsequent patterns throughout life (ontogeny), from seedlings to adults (Chacón-Labela et al., 2014; Espinosa et al., 2016). In well conserved tropical forests, limited dispersal causes aggregated patterns of seedlings around parental trees, which eventually shift to less clumped spatial structures due to negative density-dependent processes where herbivory could play a critical role (Janzen, 1970; Connell, 1971; Geßler et al., 2005; Álvarez-Yépez et al., 2014). Some studies on tropical and subtropical forests suggest that diversity is influenced by intraspecific negative density dependence at the individual tree scale, which in turn influences the relative abundance of species at the community level (Janzen, 1970; Stoll and Bergius, 2005; Chen et al., 2010; Comita et al., 2010) and such dynamics can be intensively altered by livestock grazing.

Bursera graveolens (Kunth) Triana & Planch. is the dominant tree species (above 90% of the tree cover in many stands) in many of the dry seasonal forests on the coast of Ecuador and Peru (Linares-Palomino et al., 2011) and has a high economic value (Aguirre and Kvist, 2005; Carrión-Paladines et al., 2016). Unfortunately, the intensity of deforestation and subsequent overgrazing have left the remnants in a very critical stage (Cueva et al., 2020). In the ample territory dominated by this tree species, there are almost no recruits for the last 20 years (Gusmán per obs.; Aguirre-Mendoza and Kvist, 2009). Mitigation of this dramatic impact requires range management measures and also a clear knowledge about the patterns and processes of natural recruitment and regeneration in these forests. For example, the regeneration of most tree species in the seasonally dry tropical forests of the Galapagos Islands was only achieved after removing feral goats (Hamann, 2004). A simple way for dealing with overgrazing is, therefore, facilitating forest regeneration through the establishment and maintenance for a minimum period of time of fenced zones which would avoid domestic grazing (Adler et al., 2001; Stern et al., 2002; Morales et al., 2016; Trigo et al., 2020).

Our main goal in this study is evaluating the regenerative response of *Bursera graveolens* populations after eight years of grazing exclusion, compared to free-grazing zones. For this, we analyze in detail the spatial structure of two life stages (recently recruited juveniles and adults) and the spatial association between them. Point pattern analysis (Baddeley et al., 2015) has a successful record of ecological applications (Velázquez et al., 2016; Wiegand and Moloney, 2013) which have shown that, based on appropriate null models, it allows inferring demographic processes from static maps of plant individuals (Law et al., 2009; McIntire and Fajardo, 2009). For example, point pattern analysis has been used to disentangle the effects of dispersal on population structure (Seidler and Plotkin, 2006) including its interactions with environmental microheterogeneity (Jara-Guerrero et al., 2015; Lara-Romero et al., 2016; Ramón et al., 2018), negative density dependent effects (Getzinger et al., 2008; Chacón-Labela et al., 2014), the effects of adult-

seedling facilitation (De la Cruz et al., 2008; Granda et al., 2012), or the existence of sustained population self-thinning (Kenkel, 1988).

We expected that the spatial pattern of adult trees inside and outside the fences should be similar because they were recruited before forest use intensification, while juveniles will appear in the fenced areas with structures similar to those of other natural, undisturbed populations. More specifically, we tested the following hypotheses: 1) The main perturbation excluded by fences (i.e., grazing) would not affect adult vital rates and particularly mortality, and therefore adult trees would show similar patterns inside and outside the fence. 2) The exclusion of grazing would not affect intraspecific competition among adults, so the spatial pattern of adult tree heights would be similar among fenced and unfenced plots. 3) Fenced areas would allow the recruitment of new (i.e., juvenile) individuals, which, as a consequence of limited dispersal, would appear clustered in some areas of the plot. 4) Close neighbor juveniles will experiment intraspecific competition (Comita and Hubbell, 2009), leading to self-thinning and fine scale inhibition (i.e., regular) patterns (Kenkel, 1988). 5) Intraspecific competition among juveniles will also affect growth; this will cause negative dependence in the spatial distribution of juvenile's heights. 6) Competition with adults or a Janzen-Connell effect (Janzen, 1970; Connell, 1971) will increase mortality of juveniles in the neighborhood of adult trees (Comita and Hubbell, 2009) leading to repulsive spatial patterns and negative spatial dependence between the heights of juveniles and adults.

2. Materials and methods

2.1. Study site and species

This study was conducted in the Zapotillo county (cantón Zapotillo in Spanish), located in Loja province, in the southernmost tip of Ecuador. Here, dry seasonal forests dominated by *Bursera graveolens* occupy up to 5700 ha distributed in several remnants. They are part of the Tumbesian biogeographic region, one of the most important zones of plant endemism in the world (Best and Kessler, 1995). Specifically, we set our experimental plots in the Palo Santo valley (4°19'S, 80°17'W) which gets its name from the vernacular denomination of this tree species. The mean annual temperatures vary between 18 °C and 26 °C; and annual precipitation ranges from ca. 660 to 1300 mm. Climate presents two distinctive seasons, a dry one that goes from May to November and a rainy period from December to April (Espinosa et al., 2018). Many of the forest species of this dry forest suffer great anthropic pressure, for instance tree species such as *Handroanthus chrysanthus*, *Terminalia valverdeae* and *Loxopterygium huasango* are cut down for their valuable wood (Aguirre and Kvist, 2005) whereas browsing of goats mainly affects species such as *Bursera graveolens*, *Eriotheca ruiz*, *Cochospermum vitifolium*, among others (Cueva et al., 2020).

Bursera graveolens is a deciduous tree 8–15 m tall and up to 50 cm DBH (Morgan and José, 2013) highly appreciated for its essential oil (Aguirre-Padilla et al. 2018). It occurs in dry forests from southeastern Mexico to northern Peru, from sea level to 1500 m (Sánchez et al. 2006) becoming dominant in some areas of the Tumbesian region. It grows on dry, rocky, nutrient-poor soils (Clark and Clark, 1981; Guerrero and López, 1993), where it establishes arbuscular mycorrhizal associations (Ivette et al., 2018). Compared to other species of the dry-forest, is a relatively fast-growing species (Morgan and Jose 2013), with a life expectancy of 200 years *Bursera graveolens* is a light-demanding species that establishes in forest openings and could persist for many years (Morgan and Jose, 2013). *Bursera graveolens* produces dry-fruits (capsular drupes) from the end of April until the beginning of June (Aguirre-Mendoza, 2002), each one with an arilate seed. The seeds hang from the branches of the tree attached to a stalk and either they are eaten (i.e., dispersed) by birds, reptiles and rodents (Clark and Clark, 1981; Nogales et al., 2017) or they fall to the ground, were they stay in the leaf litter for approximately 6 months until germination starts with the new rainy season (Morgan and Jose, 2013). Its conservation status is

considered as “least concern” by the IUCN (Samain et al., 2019), although it is potentially threatened by a decline in habitat quality related to land use change, habitat fragmentation and the extraction of wood and resins (Samain et al., 2019).

2.2. Data collection and processing

Within the Palo Santo valley, a representative fraction (35 ha) of the *Bursera graveolens* forest was fenced off in 2010 by the International Foundation for Nature and Culture (<https://natureandculture.org/>). The fence, which excludes the presence of cattle, goats and white-tailed deer (*Odocoileus virginianus*), is made of 9 lines of barbed wire, with a distance between posts of around 75 cm, and it has an average height of 1.5 m. This fence was installed as an urgent measure trying to guarantee the conservation of this dry forest and reversing its regeneration collapse. In 2018, eight years after the installation of the fences, we established a 100 × 100 m plot (F1) in the more accessible zone of the exclusion area, and then we located another two (F2 and F3) in a way to avoid any plot being less than 300 m apart from each other (this is about the maximum distance that can be achieved between three 100 × 100 m plots within the fenced area: see Fig. 1). We established another three plots (U1 to U3) outside of the fenced area, following the same 300 m rule but also avoiding that they were more than 250 m apart from the fence. Note that although the existence of just one fenced zone may suggest that the plots are pseudoreplicates, all the main tests in our paper are for models fitted independently to the spatial patterns found in each plot and, therefore, the interpretation of their results would be the same, were they pseudoreplicates or not.

In each plot, all individuals ≥30 cm tall were mapped using a total station, Leica TS02-5 Power with an accuracy of <5 cm. We also

recorded the DBH of all individuals with DBH ≥ 5 cm and height. Height was recorded using a TruPulse 360° compact electronic laser hypsometer for individuals ≥1.5 m in height, and with a tape measure for individuals <1.5 m. Since the population structure is clearly bimodal in the fenced area, with two completely distinct, non-overlapping size classes (Fig. 1), the population was divided into two life stages: adults, which are the trees ≥4 m in height, and juveniles, which are the trees <4 m in height.

To study the influence of adults on juveniles, several “maps of influence” were computed from the point pattern of adults in each plot (supplementary Fig. S1). We divided each plot in 90,000 small quadrats (each 0.3 × 0.3 m; hereafter called “spatial locations”). For each spatial location *u* in each plot (including locations occupied by juveniles), we computed the following measures: distance to the nearest adult tree (NAD), the influence of adult trees (IA_u), the influence of adult’s height (IH_u), and the weighted influence of adult’s height (IH_w). Mathematical details are supplied in supplementary material (supplementary Fig. S1)

2.3. Spatial analysis tools

To describe the spatial pattern of adult and juveniles’ trees, we used statistical point pattern analysis tools and, in particular, on univariate and bivariate versions of Ripley’s K-function (Ripley, 1976; Illian et al., 2008) and pair-correlation function (Stoyan and Stoyan, 1994; Wiegand and Moloney, 2013; Illian et al., 2008). $\lambda K(r)$, where λ is the intensity (i.e., density) of a homogeneous point pattern and $K(r)$ the univariate K-function, estimates the expected number of points within a circle of radius *r* around an arbitrary point. Similarly, $\lambda_j K_{ij}(r)$, where λ_j is the intensity of type “j” points and $K_{ij}(r)$ is the bivariate K function, estimates the expected number of type “j” points within distance *r* of an arbitrary

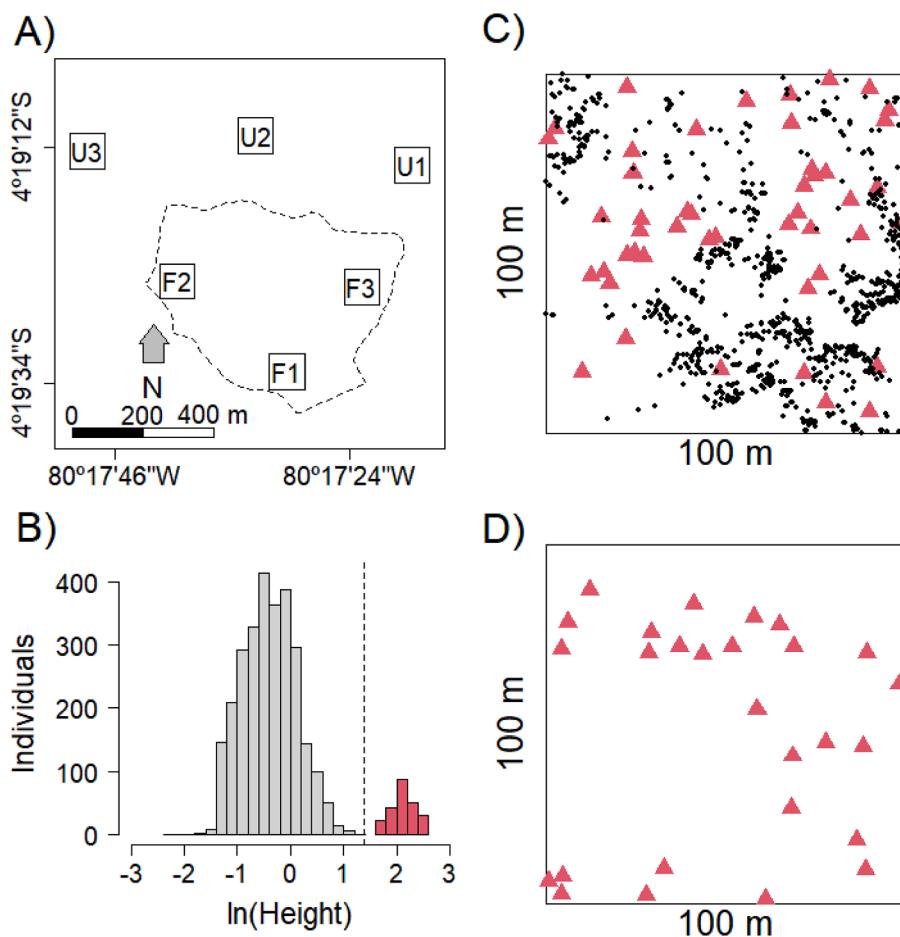


Fig. 1. A) Geographic location of fenced (F1, F2, F3) and unfenced (U1, U2, U3) plots. Dashed line indicates the perimeter of the fenced area. B) Distribution of the natural logarithm of tree height in the six studied plots. Grey bars: individuals with height < 4 m; red bars: trees with height ≥ 4 m. Dashed line represents ln(4). C) Map of *Bursera* trees in fenced plot F1. Red triangles represent individuals ≥ 4 m tall (i.e., “adults”) and black dots represent individuals < 4 m tall (i.e., “juveniles”). D) Map of *Bursera* trees in unfenced plot U1. Symbols as in C). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

point of type “i”. To facilitate visual interpretation, we used the (univariate or bivariate) L-function, i.e., the square root transformed K function: $L(r) = [K(r) / \pi]^{1/2} - r$ (Besag, 1977). The pair-correlation function $g(r)$ is the normalized derivative of the K function, i.e., $g(r) = K'(r) / (2\pi r)$. Multiplied by the pattern intensity, i.e., $\lambda g(r)$, it estimates the expected number of points at a distance approximately equal to r from an arbitrary point (Illian et al., 2008). Similarly, $\lambda_j g_{ij}(r)$, estimates the expected number of points of type “j” at a distance approximately equal to r from an arbitrary point of type “i”.

To account for spatial heterogeneity, we also used the inhomogeneous versions of the K and pair-correlation functions [$K_{inhom}(r)$ and $g_{inhom}(r)$] (see details in the supplementary material Appendix A). Instead of assuming constant intensity, inhomogeneous functions are based on inhomogeneous intensity surfaces $\lambda(u)$, where the intensity depends on the spatial location u (Baddeley et al., 2000). In this way, $\lambda(u)K_{inhom}(r)$ and $\lambda(u)g_{inhom}(r)$ represent respectively the expected number of points within and at approximately the distance r of a point in location. For completely random homogenous or inhomogeneous univariate patterns with intensity function $\lambda(u)$, $K(r) = K_{inhom}(r) = \pi r^2$, $L(r) = L_{inhom}(r) = 0$, and $g(r) = g_{inhom}(r) = 1$. For independent bivariate patterns, $K_{ij}(r) = K_{ji}(r) = K_{ii}(r) = K_{jj}(r)$ (and the same for the bivariate $g_{ij}(r)$ function). This allows using these values as baselines for contrasting the summary functions of observed patterns.

In addition to $K_{ij}(r)$ and $g_{ij}(r)$, we used also the function of the cumulative distribution of distances to the nearest different neighbor, $G_{ij}(r)$. The cumulative distribution $G_{ij}(r)$ estimates the proportion of points of type “i” which have its nearest neighbor of type “j” at a distance equal or larger than r .

To analyze the spatial distribution of heights of adult and juvenile trees, we used tools for marked point patterns (Hanisch and Stoyan, 1979). For a quantitative variable m (i.e., the “mark”) which varies throughout the points of a spatial point pattern, the mark-correlation function is defined as $k_{mm}(r) = \frac{c_{mm}(r)}{\mu^2}$, where μ is the mean of m and $c_{mm}(r)$ is the conditional mean of the product of the marks, i.e., $E_o[m_o m_r]$, of all point-pairs where o is the origin and r any point with distance r from the origin (or, in other words, the average of the product of marks of any point pair separated by a distance r) (Illian et al., 2008). It measures the spatial dependence of the marks (Baddeley et al., 2015). Values of $k_{mm}(r)$ larger or smaller than 1 indicate respectively positive and negative spatial dependence of mark values (Baddeley et al., 2015). Complementarily, the mark variogram function $\gamma(r) = \frac{1}{2}E[(m_o - m_r)^2]$ is half the conditional mean of the squared difference between the marks of all point-pairs separated by a distance r (Baddeley et al., 2015).

To analyze the dependence between the heights of juvenile and adult plants, we used a function similar to the intertype mark correlation function (Ledo et al., 2011) $k_{mm}^{ij}(r) = \frac{c_{mm}^{ij}(r)}{\mu_i \mu_j}$, where μ_i and μ_j are respectively the means of the marks of point types i and j , and $c_{mm}^{ij}(r)$ is the conditional mean of the product of marks of all bivariate point-pairs (i.e., including one point of type i and the other of type j) separated approximately by distance r . Analogously, we also computed an intertype mark variogram function, $\gamma^{ij}(r) = \frac{1}{2}E[(m_{i_o} - m_{j_r})^2]$, which estimates half the conditional mean of the squared difference between the marks of all bivariate point-pairs (i.e., pairs with one point of each type) separated by a distance r .

2.4. Statistical analysis

We used different analyses to test our hypotheses and to answer our questions about the effects of the management plans (i.e., fence) on the structure of *Bursera* populations. A summary of the research questions and the tools and null models used to answer them is presented in Table 1.

To test our first hypothesis about the lack of differences and absence of spatial structure (i.e., random pattern) for adult trees in fenced vs non-

Table 1

Research questions, statistical analyses and null models employed in the study.

Question	Statistical tool	Null models	Related figures and tables.
Adults			
Are the spatial structures of adult trees in fenced and unfenced plots similar?	$K(r)$	CSR	Table S.1 Fig. 2
Is the clustered pattern found in some adult patterns due to spatial heterogeneity, limited dispersal or both?	$K(r)$, $K_{inhom}(r)$	TP IPP, ITP	Table S.1 Fig. S.2
Does interspecific competition affect tree height?	$k_{mm}(r)$	RL	Fig. S.3
Juveniles			
Do juveniles recruit with a clustered pattern?	$K(r)$	CSR	Fig. S.4
Is the clustered pattern of juveniles due to spatial heterogeneity, limited dispersal or both?	$K(r)$, $K_{inhom}(r)$	TP, 2TP IPP, ITP,	Fig. 3; Table S.2 Table 3
Does intraspecific competition affect the spatial pattern of juveniles?	$K(r)$	CSR	Fig. S.4
Does intraspecific competition affect the spatial distribution of juvenile's height?	$k_{mm}(r)$, $\gamma(r)$ GLMM	RL	Fig. 4 Table 4
Does competition with adults affect the spatial distribution of juveniles?	$G_{ij}(r)$, $K_{ij}(r)$, $g_{ij}(r)$ PPM	TS IPP _a	Fig. 5 Table S.3
Does Negative Density Dependence affect the spatial distribution of juvenile's height?	$k_{mm}^{ij}(r)$, $\gamma^{ij}(r)$ GLMM	RRL	Table 4

$K(r)$: Ripley's K function. $K_{inhom}(r)$: inhomogeneous K function. $k_{mm}(r)$: mark correlation function. $\gamma(r)$: mark-variogram function. $k_{mm}^{ij}(r)$: intertype mark correlation function. $\gamma^{ij}(r)$: intertype mark variogram function. $K_{ij}(r)$: bivariate K function. $G_{ij}(r)$: bivariate nearest neighbor distances distribution function. $g_{ij}(r)$: bivariate pair correlation function. GLMM: generalized linear mixed model. PPM: Point process modeling. CSR: complete spatial randomness. IPP: inhomogeneous Poisson process based on spatial coordinates. IPP_a: inhomogeneous Poisson process based on influence of adults. ITP: inhomogeneous Thomas process based on spatial coordinates. TP: Thomas process. TS: toroidal shift. RL: random labeling. RRL: restricted random labeling.

fenced sites, we conducted a complete spatial randomness (CSR) test on the population of adult *Bursera* trees in each of the 6 plots. For this, we computed the homogeneous, univariate $L(r)$ function for each population and compared it with the envelopes resulting from 199 simulations of a CSR null model. If our hypothesis was true, observed L functions would remain inside the envelopes at all spatial scales r . Deviations where assessed with a goodness-of-fit test (Loosmore and Ford, 2006). Similar to post hoc test, as several plots deviated from CSR and showed symptoms of aggregation (i.e., $L(r) > 0$ for some spatial scales), we fitted three kind of point process to each of the patterns: 1). We first fitted an inhomogeneous Poisson point process based on spatial coordinates (i.e., on a trend surface, Baddeley et al., 2015), as an apparently aggregated pattern can be a consequence of spatial heterogeneity (Wiegand and Moloney 2013). 2) We fitted also a Thomas point process (i.e., a cluster process). 3) We finally fitted an inhomogeneous Thomas process (i.e., a process considering both clustering and the effects of heterogeneity). For each plot we chose the best model of the three (inhomogeneous Poisson, Thomas and inhomogeneous Thomas) i.e., the model with the smallest AIC (AIC based on the sum of residuals and the number of parameters in each model: Shen et al., 2009; Jara-Guerrero et al., 2015 This coincided with the model which best performed in a goodness of fit test (Loosmore and Ford, 2006).

To test our second hypothesis, about the effects of intraspecific competition on the spatial distribution of adult heights, we computed mark-correlation functions for each plot. We tested the observed functions against a null model of random labeling (i.e., permutation of heights through the different spatial points). Model fitting was assessed

with a goodness of fit test (Loosmore and Ford, 2006).

To test our third hypothesis about the clustered spatial structure of the populations of juvenile trees we first conducted a complete spatial randomness (CSR) test on the population of juvenile *Bursera graveolens* trees in each plot. The procedure was the same than for the CSR test of adult trees. If our hypothesis was true, observed L functions would appear above the upper envelope at least for some spatial scales r . To investigate the possible causes of the aggregated patterns (as, in fact, it deviated from CSR and showed symptoms of aggregation in all plots), we fitted the same point processes that we fitted previously for adults: inhomogeneous Poisson process based on spatial coordinates, Thomas process, and inhomogeneous Thomas process based on spatial coordinates. As the results of fitting the Thomas process revealed symptoms of additional clustering, we also fitted homogeneous nested double cluster Thomas processes (Wiegand et al., 2007, 2009).

For each plot we chose the model with the smallest AIC (Jara-Guerrero et al., 2015), which also coincided with the model which best performed in a goodness of fit test (Loosmore and Ford, 2006).

To test our fourth hypothesis about the effects of juvenile, intraspecific competition on the survival of juveniles, we scrutinized the results of the CSR test obtained in the previous analysis for evidences of fine scale inhibition (i.e., for values of the L function smaller than the lower envelope at small values of r). If competition affects survival, mortality of juveniles would be density dependent, generating regular patterns at fine scales. To test the effects of intraspecific juvenile competition on juvenile growth, we computed mark-correlation and mark-variogram functions for the heights of juveniles in each plot and tested the observed functions against a null model of random labeling. If competition is affecting growth, we would expect to find negative dependence among the heights of neighbor trees (i.e., the closer the trees, the smaller their heights), and therefore, lower $k_{mm}(r)$ values than expected at short r scales. In the case of size-asymmetric or symmetric competition we would expect respectively larger or smaller values than expected for the mark-variogram function at the same scales where $k_{mm}(r)$ deviated from the null model of random labeling. In addition, we assessed the effects of juvenile neighborhood on seedling height by fitting a regression model (Gaussian GLMM) to the logarithm of plant height, using as predictors both the number of neighbor juvenile plants within a circle of radius = 1 m around each focal plant and a weighted sum of the heights of neighbor juvenile plants in the same area. If juvenile intraspecific competition occurs, we expected that we would find a negative effect of both the number of juvenile neighbors and their weighted sum of heights on the height of the focal plants.

Finally, we tested our fifth and sixth hypotheses about the negative relationships between adult and juvenile plants. We first examined the joint effects of all adults on the coarse scale pattern of juveniles, i.e., on its intensity. For this, we fitted inhomogeneous Poisson (IP) models to the intensity of juveniles, following the same procedure that we followed for the models based on spatial coordinates but using in this case the measures of influence of adults previously computed (NAD, IA, IH and WIH) as predictors. If adults have a negative influence on the intensity of juveniles, these predictors would show significant negative coefficients in the IP models. Secondly, to test the effect of individual adults on the survival and/or recruiting of juveniles, we conducted tests of independence of the pattern of both age classes. For this purpose, we computed in each plot the bivariate nearest neighbor distance distribution function $G_{ij}(r)$, the bivariate $K_{ij}(r)$ function and the bivariate pair-correlation function $g_{ij}(r)$. Deviations from independence were assessed with goodness of fit tests (Loosmore and Ford, 2006) for a null model of random toroidal shifting of adult tree positions (Lotwick and Silverman, 1982). If adults exert an individual negative influence on the survival or recruitment of juveniles, we would expect to find negative deviations, at least for fine scales r , in the test of independence. Third, to test the effects of the competition of adults (or other negative density dependent mechanism related to them) on the growth of juveniles, we computed

the inter-type mark correlation function $k_{mm}^{ij}(r)$ and the inter-type mark variogram function $\gamma^{ij}(r)$ with the heights of adults and juveniles in each plot. We tested the observed functions against a null model of restricted random labeling (i.e., maintaining fixed the heights of adults and permuting the heights of juveniles). Another mechanism that could be related to the size of plants is the asymmetrical competition where there is an unequal sharing of resources as consequence of larger individuals having a competitive advantage over smaller ones (Freckleton and Watkinson 2001). If asymmetric competition is affecting the growth of juveniles, we would expect to find negative dependence among the heights of neighbor adults and juveniles (i.e., the closer the plants, the smaller their heights), and therefore, lower $k_{mm}^{ij}(r)$ values than expected and larger $\gamma^{ij}(r)$ than expected at small r scales. As an additional analysis, we assessed the effects of the adult neighborhood on seedling height by including a weighted sum of the heights of neighbor adult trees (in a circle of 10 around each focal plant, Comita and Hubbell, 2009) as an additional predictor in the GLMM for the logarithm of plant height described previously. If Janzen-Connell effects of competition between adult and juvenile individuals occur, we expected that we would find a significant negative coefficient for the weighted sum of neighbor adult heights.

Detailed descriptions of the null models, model fitting and model assessment are provided in the supplementary material (appendix A). All analyses were conducted in R (R Core Team, 2020). Point pattern analyses, including preparation of spatial covariates, simulations and model selection based on AIC were mainly performed with the packages spatstat (Baddeley et al., 2015), ecespa (De la Cruz, 2008), and selectsp (De la Cruz, 2015). In all spatial analyses, we computed summary functions from $r = 0$ to $r = 25$ m, with 0.1 m steps. All tests were based on 199 simulations of the appropriate null model. GLMM analysis was conducted with lmer() function in package lme4 (Bates et al., 2012). We used packages spdep and spatialreg (Bivand et al., 2013) to compute maximum distance graph and Moran eigenvectors which were included as covariates in the GLMMs. Hierarchical clustering of juvenile coordinates and group definition (i.e., random factor) for the GLMM analysis were performed with functions dist(), hclust() and cutree() of package stats (R Core Team, 2020). Packages spdep and pgirmess (Girardoux, 2018) were used to test for residual autocorrelation (Moran test and Moran correlogram based on distance bands).

3. Results

We mapped a total of 3006 individuals in the six plots. The mean number of adult trees in the fenced and non-fenced plots was 51 and 30, respectively (Table 2). There were no significant differences between their density inside and outside the exclusion zone (Mann-Whitney test, $U = 8$, $p = 0.20$); mean tree height of adults was 8.6 m. There were not differences of adult tree height between fenced and unfenced plots (Welch two sample t -test for the logarithm of three height, $t = 1.264$, $p = 0.21$).

The spatial pattern of adult trees varied idiosyncratically among plots and showed symptoms of complete spatial randomness (Fig. 2, F3, U1, U3), virtual aggregation (Fig. 2, F1 and F2), or clustering (Fig. 2, U2).

Model fitting and selection, however, confirmed that these tree patterns were best described by a cluster process (Fig. S.2, Table S.1), although the size of the clusters (~16.3 vs. 8.5 m) and the number of trees per cluster (~42 vs. 24 m) were almost twice as large in the two fenced than in the unfenced plot. Mark variogram analyses showed that the distribution of adult heights was spatially independent in both the fenced and unfenced plots (Fig. S.3).

We found 2765 juveniles, only in the three fenced plots, with densities varying more than 100% from one plot to another (Table 2). Average juvenile height was 0.76 m. CSR tests showed that juveniles recruited with an aggregated pattern (Fig. S.4). Inhomogeneous Poisson

Table 2
Summary information of the plots.

Plot	Fenced	N	Height (m)	DAP (cm)	Dens (N m ⁻²)	Nndist (m)
Juveniles						
F1	Yes	919	0.7 ± 0.3	na	36.90	0.9 ± 1.1
F2	Yes	455	0.9 ± 0.5	na	17.46	1.5 ± 1.5
F3	Yes	1391	0.8 ± 0.4	na	55.99	0.9 ± 0.8
Adults						
F1	Yes	46	9.4 ± 1.8	25.9 ± 6.7	1.88	6.7 ± 5.2
F2	Yes	70	8.2 ± 1.7	24.8 ± 7.5	2.86	4.9 ± 3.9
F3	Yes	34	9.6 ± 2.7	26.0 ± 7.8	1.35	9.4 ± 5.8
U1	No	27	7.9 ± 1.6	27.0 ± 4.8	1.06	9.4 ± 4.5
U2	No	47	7.7 ± 2.3	22.3 ± 7.8	1.85	6 ± 5.6
U3	No	17	10.2 ± 1.6	30.3 ± 7.8	0.66	15.7 ± 8.1

N: number of individuals; DAP: diameter at breast height; Dens: density of individuals (individuals m⁻²); Nndist = average distance to the nearest individual; na: not available

models based on spatial coordinates confirmed the existence of a spatial trend on the distribution of juveniles (Table 3). Model fitting and selection showed that, in addition to the virtual aggregation caused by spatial heterogeneity, limited dispersal was also responsible for juvenile distribution (Fig. 3; Table S.2), with all plots best described by an inhomogeneous cluster process. The size of the juvenile clusters varied between 7 and 9 m, and included between 46 and 128 plants per cluster.

We found 2765 juveniles, only in the three fenced plots, with densities varying more than 100% from one plot to another (Table 2). Average juvenile height was 0.76 m. CSR tests showed that juveniles recruited with an aggregated pattern (Fig. S.4). Inhomogeneous Poisson models based on spatial coordinates confirmed the existence of a spatial trend on the distribution of juveniles (Table 3). Model fitting and selection showed that, in addition to the virtual aggregation caused by spatial heterogeneity, limited dispersal was also responsible for juvenile distribution (Fig. 3; Table S.2), with all plots best described by an inhomogeneous cluster process. The size of the juvenile clusters varied between 7 and 9 m, and included between 46 and 128 plants per cluster.

CSR tests did not show any signs of fine scale inhibition among juveniles, suggesting the lack of intraspecific competition on survival

Table 3
Significance test after stepwise regression in the inhomogeneous Poisson model of juveniles.

Plot	Term	LR Chisq	Df	p-value
F1	x	134.931	1	<2.2e-16
	y	56.778	1	4.878e-14
	x:y	99.207	1	<2.2e-16
F2	x	2.8995	1	0.08861
	y	29.1044	1	6.858e-08
	x:y	4.6862	1	0.03041
F3	x	52.005	1	5.535e-13

Statistic (Likelihood Ratio Chi square), degrees of freedom (Df) and p-value (p-value) for likelihood-ratio chi-square tests of the terms retained after stepwise regression in the inhomogeneous Poisson model based on coordinates for the intensity of juveniles for the tree fenced plots (F1 to F3. x, y, x:y: spatial coordinates and their intersection, respectively).

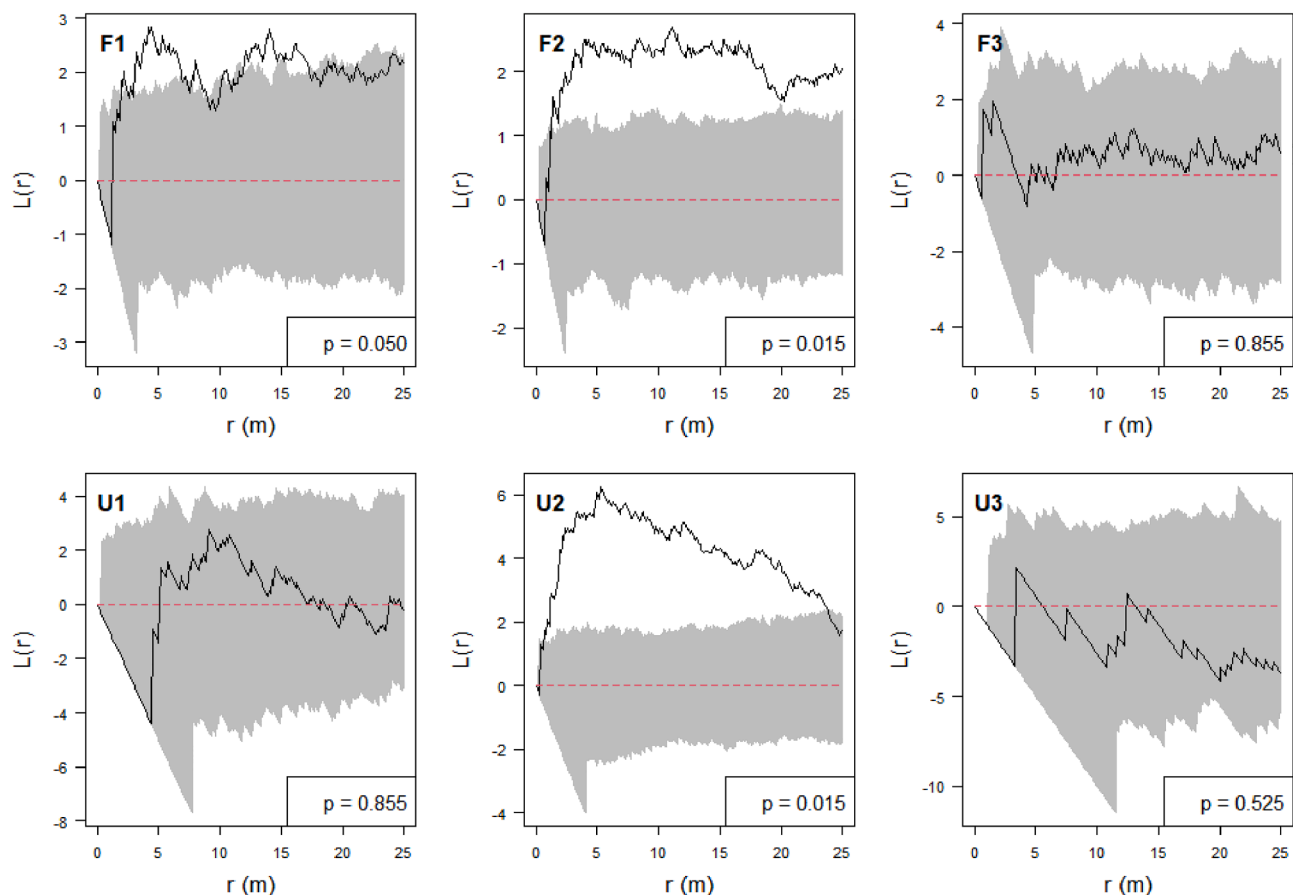


Fig. 2. CSR test of *Bursera graveolens* adult trees in fenced (F1 to F3) and unfenced (U1 to U3) plots. Grey areas represent the envelopes of 199 simulations of a homogeneous Poisson null model. Adjusted p-values (by false discovery rate) of a goodness of fit test are provided in the inset.

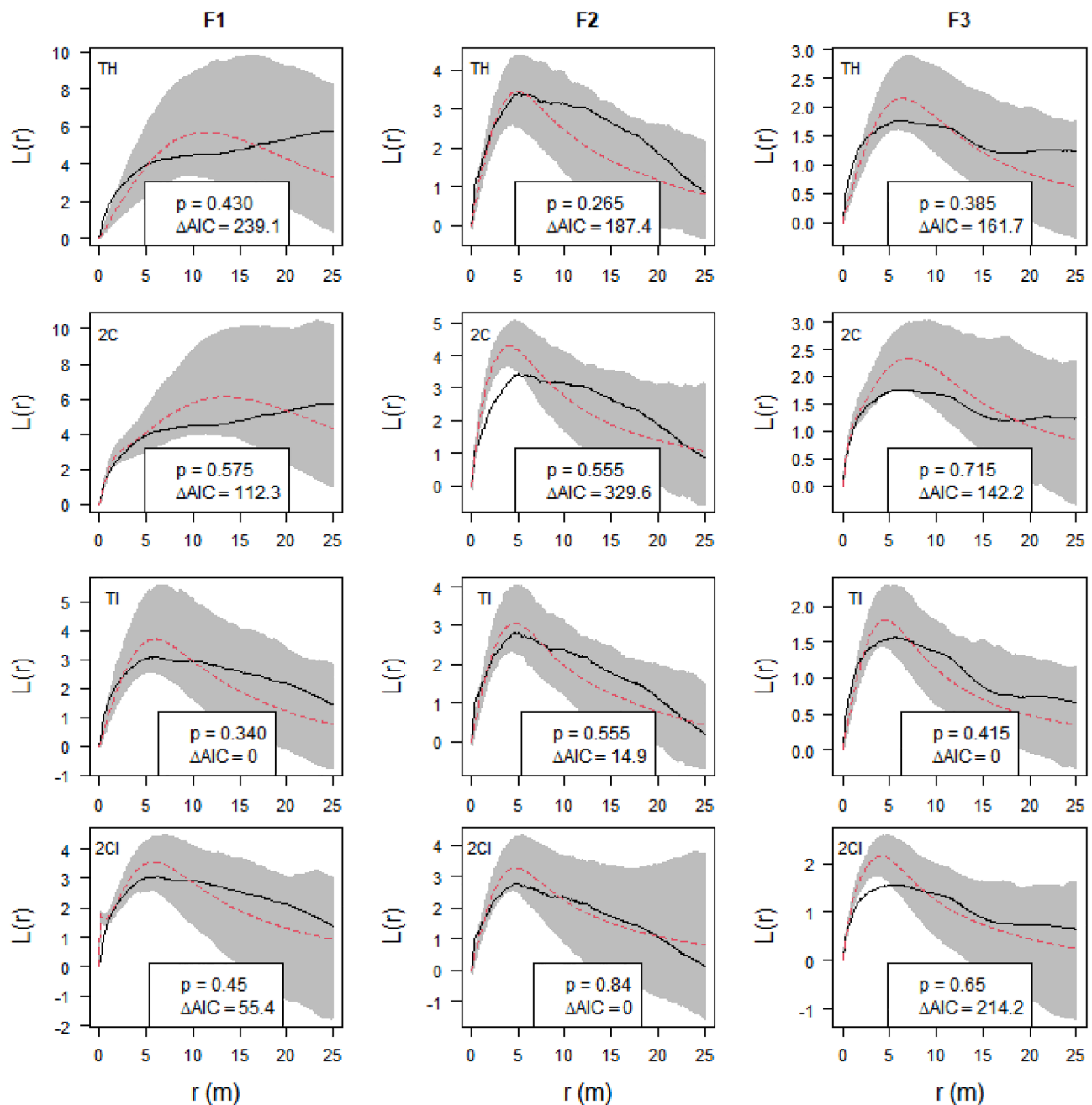


Fig. 3. Envelope tests for four different point processes fitted to the pattern of *Bursera graveolens* juveniles in the three fenced plots (F1 to F3). TH: homogeneous Thomas process. 2C: Homogeneous double Poisson cluster process. TI: inhomogeneous Thomas process based on spatial coordinates. 2CI: Inhomogeneous double Poisson cluster process based on spatial coordinates. Black lines represent the homogeneous (TH, 2C) or inhomogeneous (TI, 2CI) observed L function. Grey areas represent the envelopes of 199 simulations of the fitted point process. Red, dashed lines, represent the average of the L functions for the simulated patterns. p (inset): p-values of a goodness of fit test. ΔAIC: Difference of AIC (Akaike Information Criterion) with the best fitted point process. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(Fig. S.4). Even more, random labeling tests on the mark-correlation and mark variogram functions showed respectively positive spatial dependence and lower variation of juvenile height that expected (Fig. 4).

Similarly, GLMMs showed a positive effect of the weighted sum of neighbor juvenile heights, but a negative one of the numbers of juvenile neighbors on the height of each juvenile (Table 4).

The restricted random labeling tests on the inter-type mark-correlation and inter-type mark variogram functions showed respectively negative spatial dependence and higher differences than expected for the heights of pairs of juvenile and adults separated for distances up to 10 m (Fig. 4). The GLMM showed also a negative effect of the weighted

sum of heights of neighbor (10 m) adults on the height of juvenile individuals.

Inhomogeneous Poisson processes based on measures of adult influence showed a negative effect of adults on the intensity of juveniles (Table S.3). Independence tests with $G_{ij}(r)$, $g_{ij}(r)$ and $K_{ij}(r)$ consistently showed a spatial repulsion between the pattern of juvenile and adults, with an area of exclusion around adults of 6–8 m (Fig. 5).

4. Discussion

Overgrazing is critical for *Bursera graveolens* dynamics and viability,

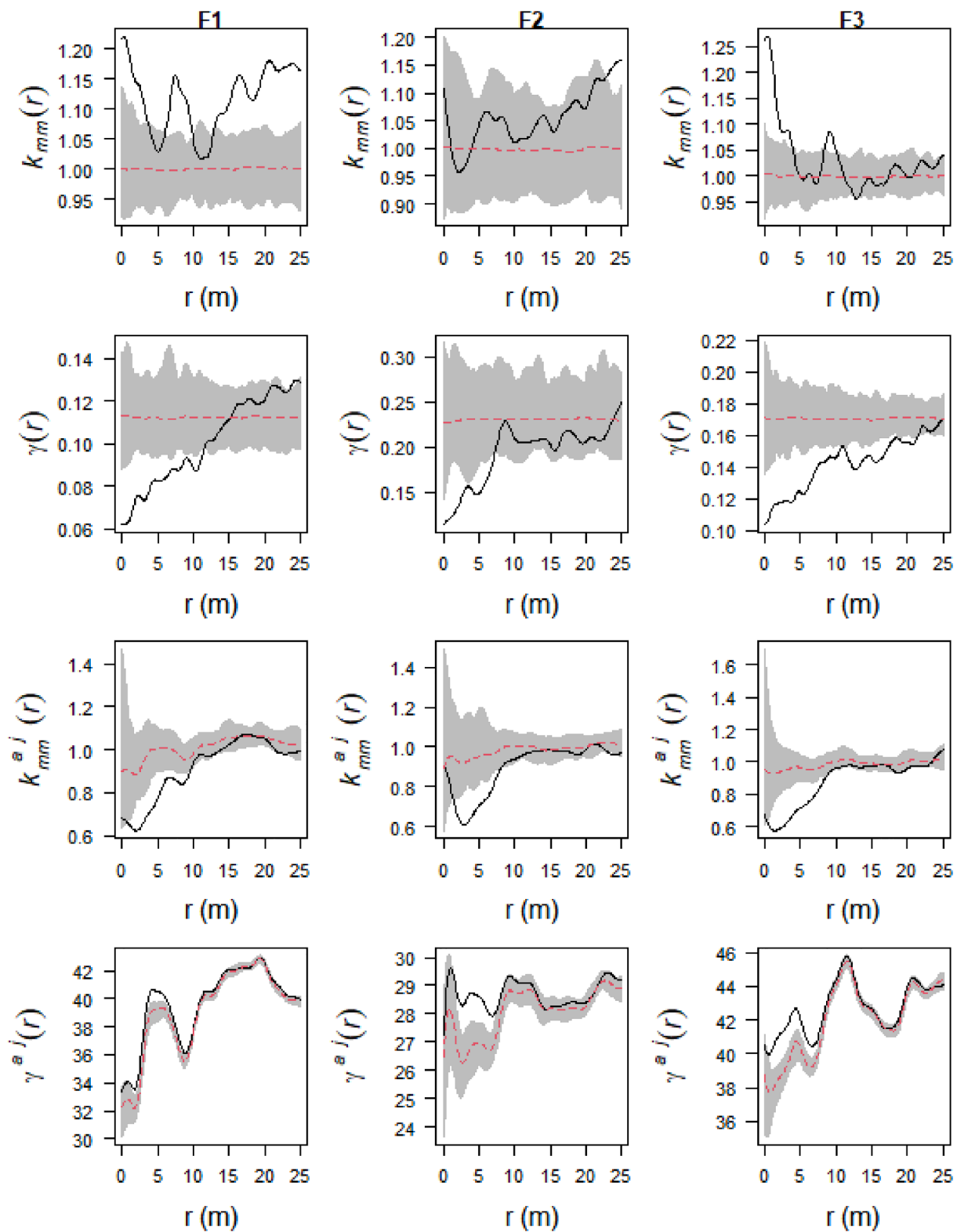


Fig. 4. Random labeling test of the spatial distribution of plant heights for juveniles of *Bursera graveolens* in the fenced (F1 to F3) plots. 1st row ($k_{mm}(r)$): mark correlogram function. 2nd row ($\gamma(r)$): mark variogram function. 3rd row ($k_{mm}^{a,j}(r)$): inter-type mark correlogram function. 4th row ($\gamma^{a,j}(r)$): inter-type mark variogram function. Black lines represent the observed mark correlogram or mark correlogram function of the heights of adult trees and juveniles. Grey areas represent the envelopes of 199 simulations of a null model of random labeling ($k_{mm}(r)$ and $\gamma(r)$) or restricted random labeling ($k_{mm}^{a,j}(r)$ and $\gamma^{a,j}(r)$) of juvenile heights. Red, dashed lines, represent the average of the functions for the simulated patterns. In all cases, the goodness of fit test was significant (false discovery rate adjusted p -values = 0.005). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Likelihood-ratio test for the GLM of juveniles' height.

Term	LR Chisq	Df	p-value	Coefficient	S.E.
Number.j1	8.82	1	0.0030	-0.04009	0.01350
Height.j1	20.96	1	<0.0001	0.05335	0.01165
Height.a10	76.60	1	<0.0001	-0.10494	0.01199
Plot	162.32	2	<0.0001		
fitted(sevm)	356.72	34	<0.0001		

Statistic (Likelihood Ratio Chi square), degrees of freedom (Df) and p-value (p-value) for likelihood-ratio Chi-square tests of the terms in the GLM model of the log-transformed juvenile height. Coefficient: fitted coefficient. S.E.: standard error. Number.j1: scaled number of neighbor juvenile plants within 1 m around each focal juvenile plant. Height.j1: scaled sum of neighbor juvenile heights (weighted by the distance) within 1 m around each focal juvenile plant. Height.a10: scaled sum of neighbor adult heights (weighted by the distance) within 10 m around each focal juvenile plant.

since it directly affects the recruitment of this dominant tree species, causing a total collapse in its regeneration and, consequently, in this type of dry seasonal forest. Numerous juvenile plants were found in the tree plots located within the fenced area, in contrast with the tree plots outside the fence where regeneration was null. In addition to this, juvenile populations were structured as it would be expected for natural, unperturbed populations, confirming the recovery of the ecological processes disrupted by decades of grazing. Although three plots per treatment may seem scarce, note that they represent about a 10% of the extension of the fenced area. Additionally, the absence of *Bursera* regeneration is pervasive across the whole Palo Santo Valley (personal observation).

As we had hypothesized, juveniles appeared clustered (with cluster diameters between 7 and 9 m, between 46 and 127 individuals per cluster, and densities of 0.7–3.0 juveniles m^{-2} in the clusters), confirming the limited dispersion of *Bursera* seeds. We found, however, that this aggregated pattern was in part a response to spatial heterogeneity (Tables 3, S.3), as it occurs also in other tropical forests (Jara-Guerrero et al., 2015; Ramón et al., 2018). Recent studies suggested that the effects of these two processes (dispersion and habitat filtering) usually overlap at fine spatial scales (Lin et al., 2011; Shen et al., 2009).

We found that adults affected negatively the distribution of juveniles both at coarse (i.e. across the plot) and also at fine scales (i.e., in the local neighborhood). For example, the average distance for a juvenile to the nearest adult was 9.8 m, and the number of juveniles within 10 m of adult trees was much smaller than expected (Fig. 5). This could be caused either by direct, asymmetric competition with adults (e.g. Barberis and Tanner, 2005) or by a Janzen-Connell-like effect (Janzen, 1970; Connell, 1971), i.e., a reduction in survival of individuals dispersed or recruited near parent trees as consequence of seed predators, herbivores and pathogens. In fact, although *Bursera* seeds could germinate without passing throughout the digestive tract of an animal disperser (Morgan and Jose, 2013; Nogales et al., 2017), it has been reported that seeds fallen directly under the crown of parent trees are predated by ants and rodents before germinating (Morgan and Jose, 2013) and that only few seeds remain under parent trees at the end of the dry season (Clark and Clark, 1981). In addition, the arbuscular mycorrhizal associations that establishes *Bursera graveolens* (Ivette et al., 2018) offers scarce protection against other antagonistic fungi that accumulate near conspecifics and may contribute to the strong negative density dependence detected (Bennett et al., 2017; Sasaki et al., 2019). Besides, being a light-demanding species, seedling and juvenile growth is favored in gaps, far from the shade of their parent trees. Actually, the inhomogeneous Poisson models based on the influence of adult trees showed a negative influence of both the number and the height of adult neighbors on the density of juveniles (Table S.3). The negative effect of adults not only affected the recruitment but also the growth (estimated by the height of individual juveniles; Table 4), which suggests that asymmetric adult-juvenile competition for light is also occurring. In

particular, the negative effect of adult height on the growth of juveniles seems to operate, at least, up to a distance of 10 m (Fig. 4).

In contrast, intra-juvenile competition seems to be much weaker. We found neither evidence for juveniles self-thinning (Fig. S.4), nor a negative effect of the height of other neighboring juveniles on their growth (Table 4). Although some studies have shown that conspecific seedling crowding may decrease survival (e.g., Comita and Hubbell, 2009), this seems to be more related to negative density dependence than to intraspecific competition (Paine et al., 2008). In fact, we found a positive effect of the height of juvenile neighbors on the growth of other juveniles (Table 4). In particular, in plots F1 and F3, we found positive spatial dependence for juvenile height, i.e., larger heights than expected for juveniles separated by less than 5 m (Fig. 4). In all fenced plots, the mark variogram showed smaller height variability than expected for juveniles separated less than 10 m (distance which coincides with the size of clusters fitted for the inhomogeneous Thomas processes, Table S.2), which definitely discards asymmetric competition among juveniles, and together with the results of the mark-correlation function, suggest conspecific positive density dependence (hereafter CPDD; Aubier, 2020). Although not common, positive spatial dependence has been found in other tropical forests and in a variety of ecosystems (e.g., Matthies, 2003; Eränen and Kozlov 2008; Andersen, 2009; Fajardo and McIntire, 2011; Calder and St Clair, 2012; Pranchai et al., 2017). CPDD is usually explained as a response to favorable environmental patches (e.g., Andersen, 2009) or to facilitation by sharing symbiotic microorganisms (e.g., rhizobia or ecto-mycorrhizal associations; Sasaki et al., 2019). In the case of *Bursera graveolens*, it seems improbable that the arbuscular mycorrhizas could be implied in the positive dependence among juveniles, and a response to favorable environmental patches (e.g., well-lit canopy gaps) may seem more plausible. The relationship of CPDD to shared, limited environmental resources seems confirmed by the negative effect of the number of close juvenile neighbors (Table 4).

The absence of clear signs of competition among juveniles implies that self-thinning in *Bursera graveolens* occurs at older ages. In fact, the spatial pattern of adult trees was either random or less aggregated (with less clusters and, much less trees per cluster) than the pattern of juveniles (Fig. 2, S.2; Table S.1). Other studies on the spatial pattern of adult *Bursera graveolens* populations in northern Peru have found also random and slightly clustered patterns (Linares Palomino, 2005). The maintenance of clustered patterns in some adult populations may be linked to the favorable sites for tree development. Clark and Clark (1981) found that one of the preferred sites for tree establishment were cracks between rocks. In addition, the spatial distribution of tree height was independent among adult trees (Fig. S.3) suggesting the absence of intraspecific competitive processes in these mature populations. Unfortunately, we did not take soil samples nor measured soil depth across the plots and therefore we cannot confirm the existence of favorable and unfavorable sites for adults, but the variability of spatial patterns found (Fig. 2) suggests a relevant role of soil heterogeneity in adult survival (Pescador et al. 2020). Note, however, that irrespective of the pattern of adult trees, the pattern of juveniles was similar among plots. This shows that even in potentially different environments there is a convergence of the restored demographic processes.

5. Conclusions

We did not find regeneration in the three non-fenced plots, but only adults which, unwittingly, are facing the extinction debt created by the collapse of regeneration (Tilman et al., 1994; Kuussaari et al., 2009). As *Bursera graveolens* stands have a slow turnover (Hamann, 2001), the severity of the situation may only seem evident too late, when most adult trees achieve its life expectancy and the whole population collapses. If no forest management measures are implemented before, this may occur during the present century, as most *Bursera graveolens* adults in the south Ecuadorian forests are probably halfway through its life span (Pucha-Cofrep et al., 2015).

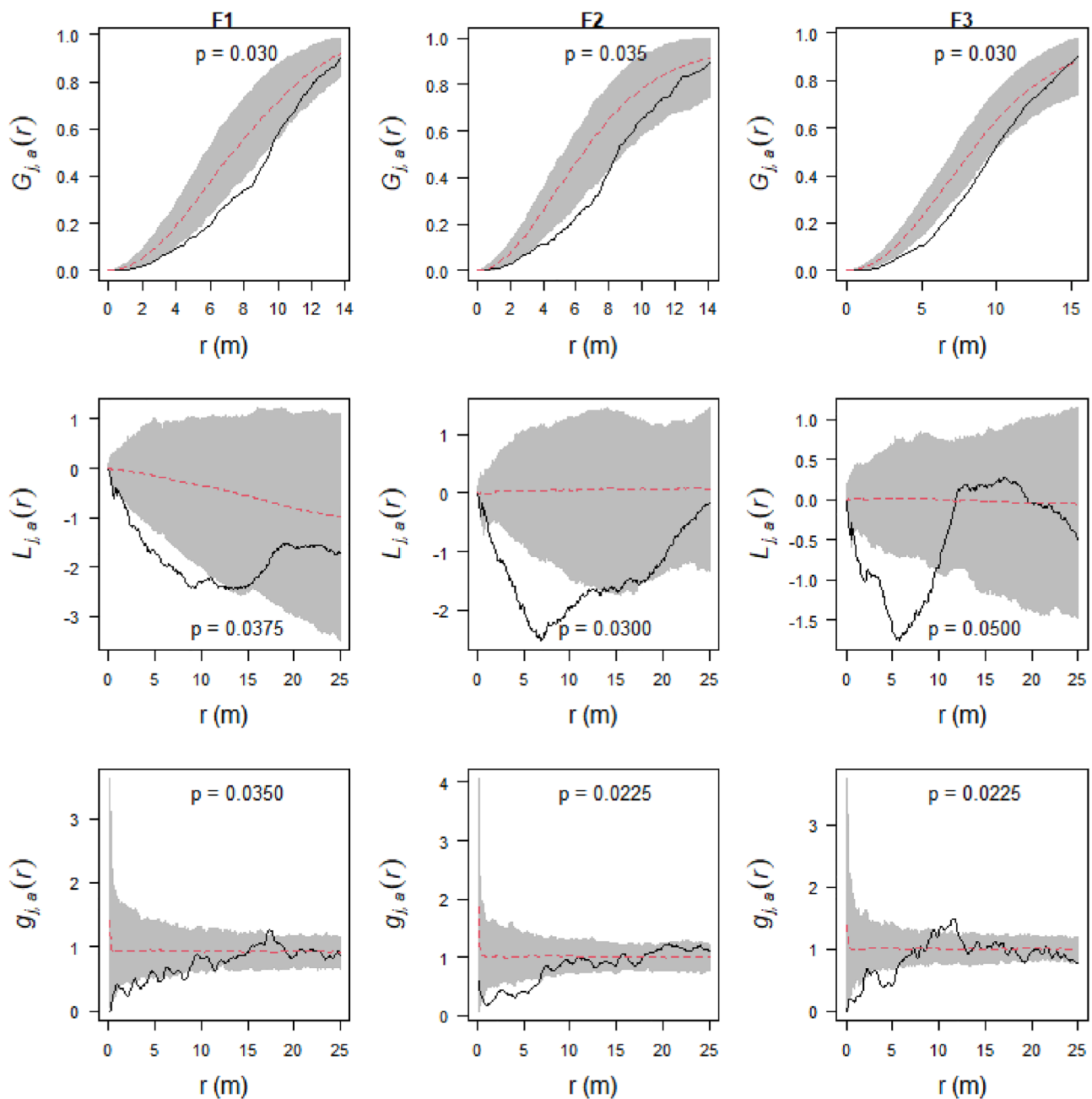


Fig. 5. Test of independence between the pattern of juvenile and adult trees of *Bursera graveolens* in the fenced (F1 to F3) plots. Upper row ($G_{j,a}(r)$): bivariate nearest neighbor distribution function. Black lines represent the observed functions. Intermediate row ($L_{j,a}(r)$): inhomogeneous bivariate L function. Lower row ($g_{j,a}(r)$): inhomogeneous bivariate pair-correlation function. Grey areas represent the envelopes of 199 simulations of a null model of toroidally shifting the pattern of adult trees. Red, dashed lines, represent the average of the functions for the simulated patterns. Values in the panels indicate the adjusted p -values (by false discovery rate) of a goodness of fit test for the interval between $r = 0$ and $r = 15$ m. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Our study shows that a simple and cheap management action such as fencing is able to reverse the negative effects of decades of free-range grazing on the dynamics of *Bursera graveolens* in just a few years. All disrupted demographic processes (dispersal, recruitment, competition) were restored and a relevant density of juvenile trees recruited efficiently within the fenced area, which contrasts with the null regeneration outside the fence. This suggests that the implementation of a system of rotation of fenced areas with periods of 8–15 years could lead to the installation and growth of new recruits with enough size to avoid being grazed and to guarantee local persistence, sustainability and conservation of this valuable forest species. Finally, it is important to note that while fencing promotes the regeneration of *Bursera graveolens*, it may

hinder the regeneration of other important species such as *Chloroleucon mangense*, *Senna mollissima*, *Piptadenia flava*, and *Caesalpinia glabrata*, dispersed by ungulates (Jara-Guerrero et al. 2018), which are also favored by livestock grazing. In forests where these species coexist with *Bursera graveolens*, it could be necessary to implement alternative management measures.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119592>.

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