

# A flash in the pan? The population dynamics of a dominant pioneer species in tropical dry forest succession

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## Abstract

Globally, around half of all tropical forests are secondary communities which are recovering from previous disturbances. In these communities, dominant pioneers play a critical role in the successional dynamics due their ability to modify the environment, and thus to facilitate or hinder the performance of other species. In this study, we examined the population dynamics of the dominant pioneer species, *Mimosa acantholoba* var. *eurycarpa*, in a tropical dry forest during the process of secondary succession. We collected data from permanent plots over a period of 13 years and used integral projection models to analyze the vital rates and changes in population size. Most vital rates were negatively related to successional age, with resprouting, survival and recruitment of individuals responding more strongly, and individual growth rate more weakly. These vital-rate trends translated into significant variation of population size over succession, with a maximum size at year four and a rapid decline thereafter. Overall, our findings suggest that this species benefits from its ability to display a large number of resprouts in very early stages of succession, contributing to the rapid increase in population density. However, as succession unfolds, a lack of resprouting and a decline in survival reduce its population size, to the point of local extinction. These results highlight the importance of resprouting in the early dynamics of tropical dry forest communities recovering from disturbance.

## KEYWORDS

dominant species, integral projection model, pioneer species, secondary succession, tree demography

## 1 | INTRODUCTION

Over more than a century a widespread process of land use change has taken place worldwide, by which native ecosystems, mainly forests, have been replaced by

agricultural fields (Lambin & Meyfroidt, 2011; Runyan & D'Odorico, 2016). In tropical regions, where swidden agriculture is often practiced, agricultural fields are usually abandoned after a few years of use due to a reduction in their productivity and yield (Aide et al., 2000). After

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land abandonment, a process of secondary succession starts, leading to vegetation cover recovery (Chazdon, 2014; Letcher et al., 2015). If undisturbed, the community is capable of reaching a relatively stable state in its traits, such as vegetation structure, species richness and species composition (Muñoz et al., 2021; Poorter et al., 2021). Globally, around half of all tropical forests are secondary communities which are recovering from previous disturbances (FAO, 2015), and this figure continues to increase as many native forests are being cleared, replaced and abandoned as the agricultural frontier continues to expand (Meyfroidt & Lambin, 2011).

A common pattern consisting of three stages has been recognized in tropical forest secondary succession (Finegan, 1996; Lebrija-Trejos et al., 2008; Martínez-Ramos et al., 2021; Mora et al., 2015; Rozendaal et al., 2016; Rüger et al., 2023). The first stage is characterized by the dominance of weeds, shrubs, and climbing plants. Next, the establishment of fast-growth, short- and long-lived trees characterizes a second stage, which eventually gives way to a third stage characterized by the establishment and development of the seedlings of slow-growing long-lived tree species under the canopy of the fast-growing trees. Those species that establish in early succession (pioneers) can either display a fast demographic strategy (grow, reproduce and die quickly) or have a longer lifespan (long-lived pioneers), while mature forest species, with a slow demographic strategy, establish later in succession (Rüger et al., 2023). The differential presence and abundance of species in each of the three stages is determined by the prevailing environmental conditions at each successional stage, which in turn are driven by feedback dynamics between the environment and the community (Lebrija-Trejos et al., 2011; Letcher et al., 2015; Matsuo et al., 2021; Wallace & Romney, 1980). Therefore, the presence of certain pioneer species may facilitate or hinder the performance of other species depending on how they modify the environment. Ultimately, dominant pioneers play a substantial role in a community's successional dynamics and ecosystem functioning (Grime, 1998).

Several studies have focused on secondary succession in tropical dry forests (Dupuy et al., 2012; Kennard, 2002; Lebrija-Trejos et al., 2010a; Lebrija-Trejos, Meave, et al., 2010; Mora et al., 2015; Peña-Claros, 2003; Pineda-García et al., 2013; Rozendaal et al., 2016). In these systems, the most important limiting factor is water availability (Allen et al., 2017; Murphy & Lugo, 1986), which entails low plant growth rates (Rozendaal et al., 2016), and also explains why succession in these forests is often dominated by very few drought-tolerant species (Ceccon et al., 2006; Markesteijn et al., 2011; Rozendaal et al., 2016). In particular, in the tropical dry

forest of the Nizanda region, southern Mexico, Lebrija-Trejos et al. (2008) found a 3-year-long initial successional phase characterized by shrub growth. After this stage, early successional *Mimosa acantholoba* var. *eurycarpa* trees become dominant over a few decades, creating a canopy layer that provides shade and reduces the air temperature in the forest understory, apparently allowing mature forest species to establish and eventually dominate late-successional stages.

Previous studies established *M. acantholoba* var. *eurycarpa*'s dominance, based on its high basal area and density of individuals compared to other species of the tropical dry forest of Nizanda (Romero-Pérez, 2014). However, little is known about the traits that underlie its dominance; although initially its thin leaves and high leaf dry mass content were proposed (Romero-Pérez, 2014), a recent study showed that wood anatomical traits in this species ensure efficient water conduction in the rainy season while reducing its hydraulic vulnerability in the dry season (Romero et al., 2020a, 2020b). Nevertheless, it is likely that some other aspect of its life cycle, such as its population dynamics, may be also involved in this pattern.

An important demographic process of pioneer species population dynamics in early succession is the entry of new individuals to the population. We name these new individuals recruits when they derive from seed germination and seedling establishment. Alternatively, there are individuals entering the population through the resprouting of vegetative structures (stumps or roots) that remain alive in the sites after the agricultural use of the field; we name these resprouts. The absence of reproductive individuals in early succession implies that its population dynamics necessarily depend on processes other than reproduction from mature local trees. These processes encompass seed dispersal from the surrounding forest matrix (Dent & Estrada-Villegas, 2021), the presence of a seed bank or the resprouting of remnant vegetative structures (Bartha et al., 2003; Guevara & Laborde, 1993; Purata, 1986; Vieira & Scariot, 2006). In the case of *M. acantholoba* var. *eurycarpa*, no seed bank has been found in the Nizanda tropical dry forest (Meave et al., 2012; Mena-Gallardo, 2009). Further, although seed rain was recorded for this species at the study site, the amount of seed produced was very low relative to the number of trees in the plots (Cervantes-Jiménez, 2018), suggesting that seed dispersal may only play a minor role in the establishment of a *Mimosa*-dominated canopy. What is presently known is that *M. acantholoba* var. *eurycarpa* is the species that displays more resprouts in the early successional community (Lebrija-Trejos, 2004). These resprouts, being live tissues produced by previously existing individuals, usually with a well-developed root

system, are able to grow and reproduce rapidly once anthropogenic disturbances stop, and represent a pathway for the increase in the species' representation in the community. Hence, acknowledging the contribution of resprouting may help better understand *M. acantholoba* var. *eurycarpa*'s population dynamics as a whole.

To gain insights into the role that population dynamics plays in the dominance of a pioneer species in a tropical dry forest, in this study we characterized and modeled the dynamics of *M. acantholoba* var. *eurycarpa* along a successional gradient. We did this by modeling this species' vital rates and their changes over succession using data from permanent plots originally established to represent a chronosequence, but then monitored yearly over 13 years. We then assembled these models into an integral projection model (IPM) that accounted for both resprouting and recruitment, and estimated annual finite population growth rates ( $\lambda_t$ ). We predicted that, at the onset of succession, the environmental conditions would promote *M. acantholoba* var. *eurycarpa*'s performance in the successional plots. Therefore, the population size of this species should increase during the early years of succession and decrease in later stages due to changes in environmental conditions in the forest interior.

## 2 | METHODS

### 2.1 | Study site

The Nizanda region (16°39'30" N, 95°00'40" W) is located on the Pacific watershed of the Isthmus of Tehuantepec, Oaxaca State, southern Mexico. The climate is warm, subhumid with summer rains ( $Aw_0(w)igw''$ ) and an annual precipitation of ca. 900 mm, strongly concentrated in the rainy season (mid-May to mid-October; Pérez-García et al., 2001). Tropical dry forest is the dominant vegetation type (Pérez-García et al., 2010). In this region, slash-and-burn agriculture is one of the main human activities, commonly involving the abandonment of plots after a few years of use, thus initiating a secondary succession process (Lebrija-Trejos et al., 2008).

### 2.2 | Study species

*Mimosa acantholoba* (Willd.) Poir. var. *eurycarpa* (B.L. Rob.) Barneby (synonym: *Mimosa eurycarpa*), hereafter referred to simply as *M. acantholoba* for simplicity, is a Fabaceae (Mimosoid) taxonomically complex species, represented by several varieties that occur from Western Mexico to northern Perú (Barneby 1991). The *eurycarpa* variety is endemic to the coastal region of western Mexico. In coastal Oaxaca State, this taxon is a multi-stemmed tree

reaching more than 7 m in height and up to 20 cm in diameter at breast height (DBH). The species is deciduous and the trees shed their foliage at the end of the rainy season (November–December), while fruit production spreads from July to the late November (Maldonado-Romo, 2014).

### 2.3 | Data collection

In the study area, a set of 17 permanent plots were established in 2003 to represent a chronosequence, as the times of abandonment (successional ages) in them differed, ranging in that year between 0 and more than 50 years (Brienen et al., 2009); thereafter, the permanent plots have been used to monitor community development through annual censuses of the vegetation and in this study we used the data up to 2016. Each year, individual height (m) and survival are recorded following the sampling protocol described by Lebrija-Trejos et al. (2008) and Muñoz et al. (2021); briefly, data are gathered in four 20 × 5 m transects, separated by 2 m wide corridors, each divided into four 5 × 5 m (25 m<sup>2</sup>) quadrats. At each plot, all *M. acantholoba* individuals with a DBH ≥ 5 cm are measured in all 12 quadrats (400 m<sup>2</sup>); individuals with a DBH ≥ 2.5 cm are measured in eight quadrats (200 m<sup>2</sup>), whereas individuals with a DBH ≥ 1 cm are measured in four quadrats (100 m<sup>2</sup>); all these plants represent the forest canopy. In total, 983 individuals were included in this data set. Additionally, saplings in the understory (individuals with DBH < 1 cm but height ≥ 30 cm) are measured in 4-m<sup>2</sup> subquadrats randomly placed in the transects (32 m<sup>2</sup>). We recorded 587 individuals in the understory data set, which included 230 recruits and 88 sprouts. Data of the different subquadrats were re-scaled in order to express all densities in the same area (see Muñoz et al., 2021).

We recorded reproduction data in November 2017 in 11 of the 17 permanent plots, for 124 individuals. For each individual, we recorded reproductive status and fruit set in one of the main stems. We extrapolated the fruit set per reproductive individual by multiplying the latter figure by its number of main stems. We collected a sample of 98 fruits from 13 trees, covering tree size variation, and counted the number of seeds per fruit. To relate these seeds with the saplings sampled in the understory, we used the subset of saplings that corresponded to recruits in 2018.

### 2.4 | Modeling procedure

We modeled the population dynamics of *M. acantholoba* along the successional gradient through an integral projection model (IPM; Easterling et al., 2000). IPMs allow analyzing the dynamics of populations structured by

continuous stage variables (Ellner et al., 2016). These are iterative models that describe the change of the population structure through a function  $k$ , called the kernel. They are represented through the equation

$$n_{t+1}(y) = \int_X k_t(y, x) \cdot n_t(x) dx, \quad (1)$$

where  $n_{t+1}(y)$  is the size structure of the population, consisting of the number or individuals of size  $y$  (log-height, m) at successional age (years since plot abandonment)  $t + 1$ ,  $n_t(x)$  is the size structure of individuals of size  $x$  at successional age  $t$ ,  $X$  is the range of all observed individual sizes, and  $k_t(y, x)$  is the kernel function at time  $t$ , as explained below. Note that in this study we are considering a kernel that changes from one time unit to the next as the dynamics change along succession.

Next, we decomposed the kernel into seven vital-rate functions as

$$k_t(y, x) = s(x, t) \cdot g(y, x, t) + f_1(x, t) \cdot f_2(x, t) \cdot f_3(x, t) \cdot f_4(t) \cdot f_5(y), \quad (2)$$

where  $s(x, t)$  is the probability of survival of an individual of size  $x$  at age  $t$ ,  $g(x, y, t)$  is the probability that an

individual of size  $x$  at age  $t$  has of changing to a size  $y$  at age  $t + 1$ ,  $f_1(x, t)$  is the reproduction probability of an individual of size  $x$  at age  $t$ ,  $f_2(x, t)$  is the average number of fruits an individual of size  $x$  has at successional age  $t$ ,  $f_3(x, t)$  is the average number of seeds in a fruit of a size  $x$  individual at age  $t$ ,  $f_4(t)$  is the average recruitment probability of a seed at age  $t$ , and  $f_5(y)$  is the size distribution of recruits originated from these seeds (Figure 1).

To include resprouting in the analysis, we include the additional functions  $f_6(t)$ , which represents the number of individuals recruited through resprouting at successional age  $t$ , and  $f_7(y)$ , which represents the size  $y$  of these resprouts at the time of their incorporation into the population. Thus, the IPM used has the form

$$n_{t+1}(y) = \int_X k_t(y, x) \cdot n_t(x) dx + f_6(t) \cdot f_7(y). \quad (3)$$

Each vital rate was modeled separately. To this end, we used generalized additive mixed models (GAMMs). For the binary variables,  $s$  and  $f_1$ , a logit link function and a binomial distribution were used; for the continuous function  $g$ , we used an identity link function and a normal distribution; and for the count variables,  $f_2$  and  $f_3$ , a log link function and a negative binomial distribution. In all these models, we considered as random effects the

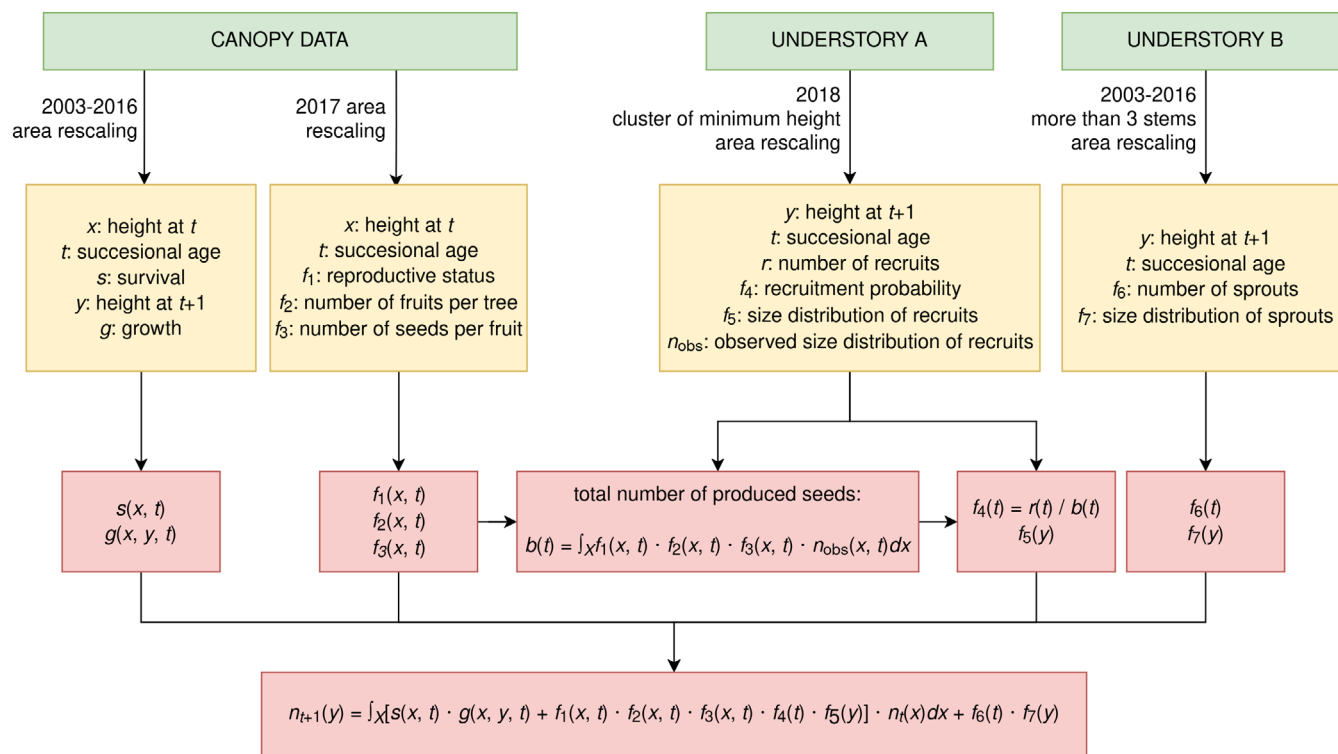


FIGURE 1 Flowchart of the modeling of vital processes of the dominant species *Mimosa acantholoba* var. *eurycarpa* in successional tropical dry forest of Oaxaca State, southern Mexico. Data from three sources (green) were filtered (unframed text), variables were extracted (yellow), and models were fitted to these data (red).



study plot, and for those vital rates for which more than one census year were available, the individual (nested in the plot) and the census year. The fitting of these models was performed in R (v. 4.1; R Core Team, 2023) using packages `gamm4` (Wood et al., 2017) and `brms` (Bürkner, 2017; Bürkner, 2018). We considered the most complex models possible that could be fitted given the limited sample size, under the assumption that this type of models best reflects the reality of a complex system (Barr et al., 2013). Among them, the best-supported model was chosen through the sample-corrected Akaike's information criterion (AICc) using the `AICcmodavg` package (Mazerolle & Mazerolle, 2017). In the case of the functions  $f_2$  and  $f_3$ , in order to prevent the selection of models that extrapolated to biologically unrealistic values, we selected among those models that predicted a maximum value of less than twice the observed maximum of fruits and seeds, respectively.

Since no establishment data were recorded in the field, we estimated recruitment probability,  $f_4$ , based on functions  $f_1, f_2, f_3$  and the observed size structures,  $n_{\text{obs}}(x, t)$ , using inverse estimation as in Gonzalez et al. (2016). For this purpose, we estimated, for each  $t$ , the total number of seeds produced per plot by individuals, distributed according to their size structure, as

$$b(t) = \int_X f_1(x, t) f_2(x, t) f_3(x, t) n_{\text{obs}}(x, t) dx. \quad (4)$$

Next, we obtained the total number of recruits from the following age  $t + 1$ . Thus,  $f_4(t)$  was estimated as the proportion between the total number of recruits and  $b(t)$ , assuming a direct relation between the observed total number of recruits and the estimated number of seeds. Following this procedure, we obtained  $f_4(t)$  values for successional ages 2, 3, 4, 10, 24, 26, 27, and 64. With these values, we fitted a spline with time as the explanatory variable.

The identification of recruits (i.e., individuals originating from the germination of local seeds) incorporated into the population at a given year was inferred indirectly from the height and number of stems of individuals in the understory. We did this by performing a  $k$ -means clustering procedure, with  $k = 6$  given by the within-clusters summed squares optimization method (Kriegel et al., 2017), using the size of individuals at their first record, and the individuals belonging to the group with the smallest sizes were classified as recruits. From the height of these individuals, the function describing recruit sizes,  $f_5(y)$ , was calculated as the associated empirical probability density. To identify resprouts, the understory individuals were filtered by considering only those with 3 or more stems in their first observation; this

criterion is similar to that used by Lebrija-Trejos (2004). From the number and heights of identified resprouts entering the population at each successional age, we obtained the function that describes the introduction of resprouts,  $f_6(t)$ , and the associated empirical probability density of resprout height,  $f_7(y)$ . Note that, since very few recruits and resprouts occur after the first years of succession, we had to assume that both  $f_5(y)$  and  $f_7(y)$  do not change throughout succession.

A discretized version of the IPM was used to obtain the annual population sizes,  $N_t$ , and the annual finite population growth rates,  $\lambda_t$ , by dividing  $N_{t+1}$  by  $N_t$ , for 100 years, a sensible age for a secondary tropical dry forest to be considered as mature (Finegan, 1996).

### 3 | RESULTS

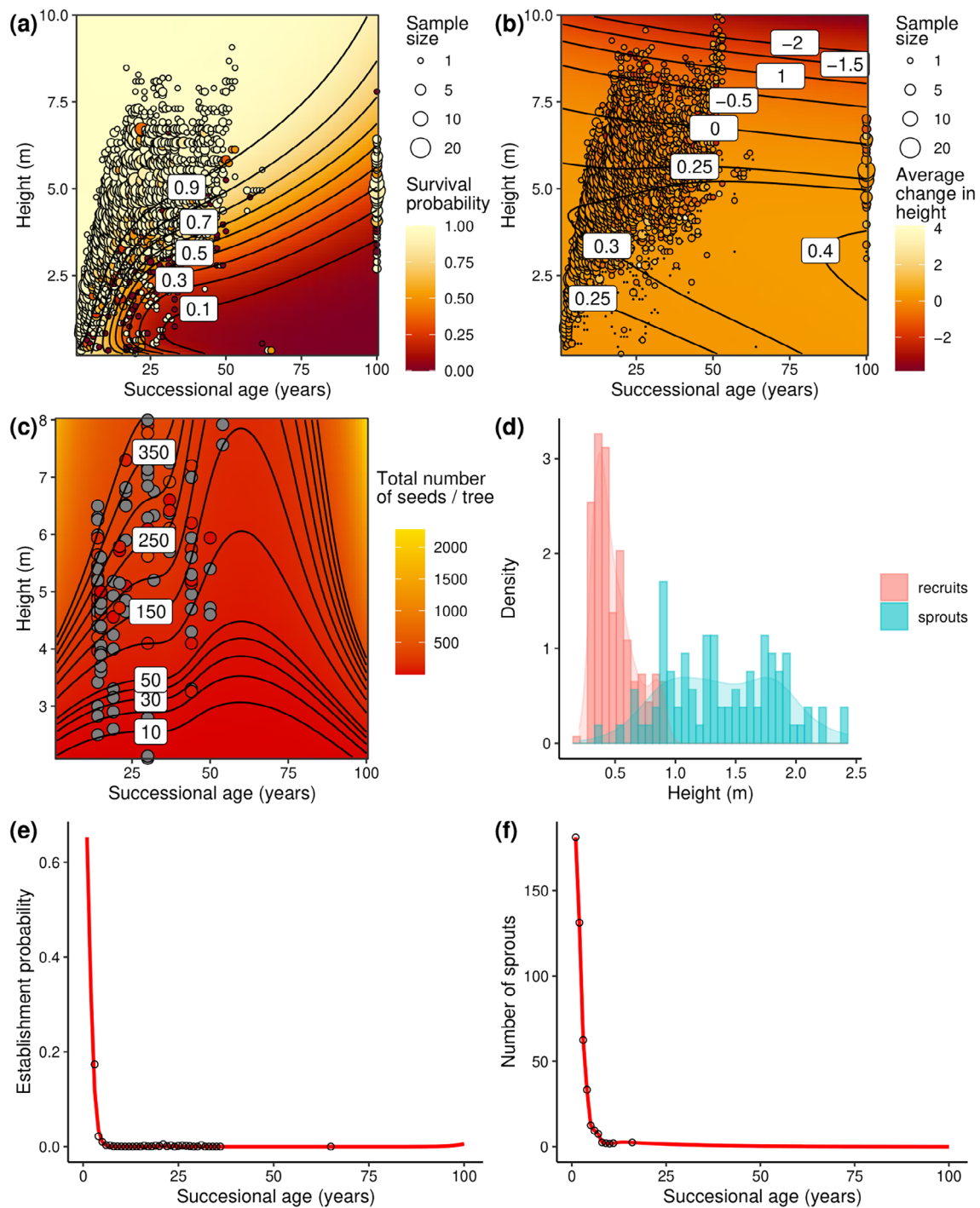
Most vital rates showed an evident relationship with successional age, with the exception of growth rate. The relationship with tree height is also clear for the survival rate and fecundity, but not for the individual growth rate. Furthermore, population size and growth rate also have marked and strong changes over succession, with high values at the onset of succession, decreasing rapidly after the first years.

#### 3.1 | Vital rates

The probability of survival,  $s$ , showed a positive relationship with tree size,  $x$ , and a negative one with successional age,  $t$  (Figure 2a). Larger trees have a higher probability of survival than smaller ones. In addition, there is an interaction between these two explanatory variables since at the beginning of succession nearly all trees, irrespective of size, have a high survival probability, whereas only trees taller than 5 m survive in the mature forest, according to the model.

The average change in height, that is, the difference between tree size at time  $t + 1$  and at time  $t$ ,  $y - x$ , displayed a negative relationship with tree size at time  $t$ ,  $x$ , and a very weak negative relationship with successional age,  $t$  (Figure 2b). Consequently, trees with heights  $> 7$  m have, on average, negative growth rates for all successional years. By contrast, trees with heights  $< 7$  m have positive growth rates throughout succession. However, this growth is very small, being at most 0.41 m per year.

Fecundity showed a positive relationship with tree height a time  $t$ , and a non-linear relationship with successional age, with this demographic component being higher at intermediate successional stages and lower both at early and advanced stages. However, the latter pattern



**FIGURE 2** Vital rates models of *Mimosa acantholoba* var. *eurycarpa* through succession. (a) Probability of survival ( $s$ ). Background color and isoclines (black lines with values shown in blank boxes) represent values predicted by the fitted model. The color and size of circles represent observed values and sample size, respectively. (b) Average change in height along succession ( $y-x$ ). The color and size of circles represent observed values and sample size, respectively. (c) Fecundity (total number of seeds produced per tree). Circles represent observed values; gray circles represent non reproductive trees. (d) Probability histograms and density functions of the heights of recruits and resprouts. (e) Establishment probability of a seed along succession. (f) Number of resprouts introduced each year.

is more evident in medium-size and large trees (Figure 2c). The average probability for a tree to reproduce was 0.34, while the maximum value was relatively low at 0.48 (Figure S1). As for total seed production per

reproductive tree, the average value predicted by the model was 231 seeds per tree (Figure 2c).

The size distributions of new recruits and resprouts,  $f_5$  and  $f_7$ , respectively, reflect the differences in size when

they enter the population (Figure 2d). While the size distribution of recruits was concentrated around 0.45 m in height, with a minimum of 0.20 m and a maximum of 0.76 m, the size distribution of resprouts had an average of 1.39 m, with a minimum of 0.34 m and a maximum of 2.43 m. In addition, the standard deviation was higher in the resprout size distribution (0.46 m), compared to the respective value of the recruits distribution (1.21 m).

The probability of establishment from seed decreased dramatically after the very first years of succession (Figure 2e). On average, the probability of establishment was very low with a value of 0.01. Only at the beginning of the succession was this value very high, with a maximum of 0.83 for the first year of abandonment, but it rapidly decreased to less than 0.1 from the fourth year onwards.

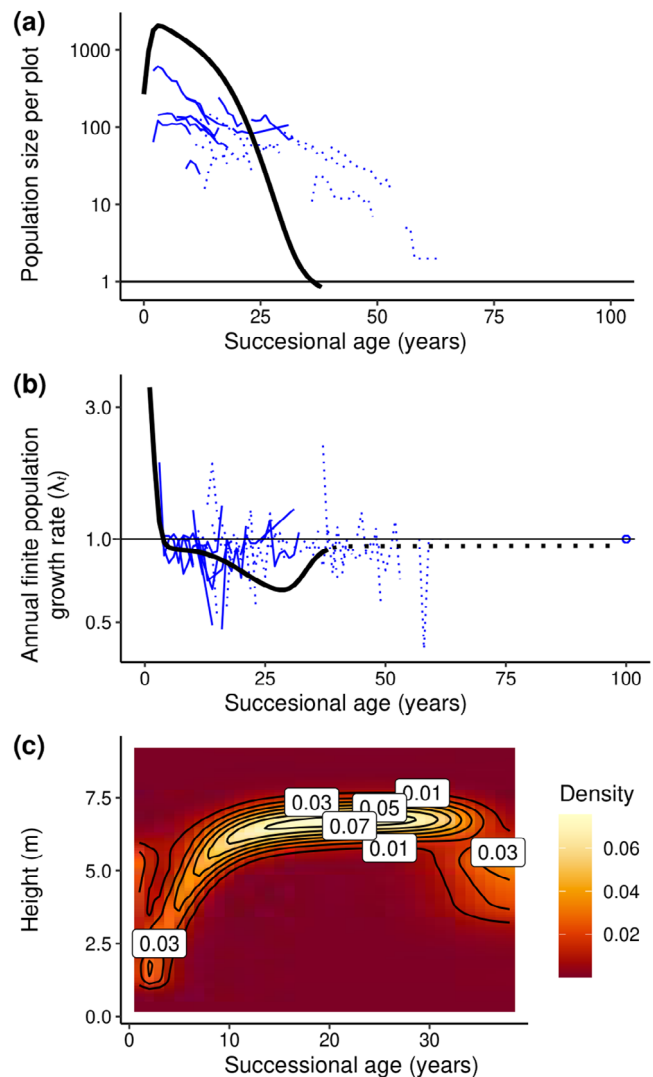
Similarly, the number of resprouts displayed per year changed drastically during the first 10 years of succession (Figure 2f). At the early stages, the maximum number of resprouts was 181. By year 10 of the succession, only 2 resprouts were included per plot, and from year 33 onwards, the number predicted by the model was less than 1.

### 3.2 | Population dynamics

Population size changed dramatically over succession (Figure 3a). In the projection, the successional process of the population starts with 238 individuals originated through resprouting as estimated by  $f_6$  at time  $t = 0$  (Figure 2d). Then, it reaches its maximum size of 2063 individuals in the fourth year; this figure consists of the original resprouts present at successional age 0 plus those resprouts and recruits added over this period (Figure 2d). After this maximum, a rapid decline begins until the population becomes locally extinct by year 38, as it reaches the one individual mark (Figure 3a). However, it must be noted that the population size predicted by the model is considerably larger than that observed in the early years of succession and considerably smaller than that observed at more advanced successional stages, even without accounting for the individuals present in the understory in those stages (dotted lines in Figure 3a).

The annual finite population growth rate,  $\lambda_t$ , also showed marked differences along the successional gradient (Figure 3b). Over the first 3 years of succession, the growth rate was positive, with a maximum value of 3.54 in the first year. From the fourth year onwards, a decrease in the population began, with the lowest growth rate in year 29, with a value of 0.65. Thereafter, a slower population decline started until reaching local population extinction (black dotted line in Figure 3b).

The population size structure also underwent important changes over succession (Figure 3c). At the



**FIGURE 3** Population dynamics attributes over succession. (a) Population size: predicted (black), observed at both canopy and understory (solid blue), and only canopy (dotted blue). (b) Annual finite population growth rate. The large blue circle represents the observed value at age 100 years; the line is dotted beyond the time for which the model predicts less than one individual, indicating extinction. (c) Predicted population size structures.

beginning of the process, the size structure was dominated by small trees. Subsequently, between approximately 10 and 30 years of succession, the population was mainly composed of trees between 5 and 7.5 m in height. Finally, from about year 30 onwards, it is again medium-sized individuals, between 5 and 3 m, that survive in the final years of the population's existence.

## 4 | DISCUSSION

The study of the population dynamics of *M. acantholoba* var. *eurycarpa* suggests that this species experiences a

negative change in the intensity of some of its vital processes as succession unfolds. Survival, establishment probability and resprouting emerge as the demographic processes that change the most during succession. Conversely, changes in fecundity and tree height are weakly related to successional age. As expected, the population grows almost exclusively during the early successional stages and consists mainly of small individuals. Despite considerable variation in population dynamics between different plots, in general, the population declines rapidly and it is finally medium-sized individuals that persist in the final stages of the population.

#### 4.1 | Successional patterns of *M. acantholoba*'s vital rates

All vital rates showed positive relationships with the height of individuals and negative relationships with successional age, with the former having larger effects than the latter. This means that in general the environmental modifications in the forest understory associated to the successional development of forest structure (Lebrija-Trejos et al., 2011) are detrimental to the demographic success of *M. acantholoba*, although not all vital processes are affected with the same intensity. These results are consistent with previous observations on the performance of this species in the successional stands (Lebrija-Trejos et al., 2008; Romero-Pérez, 2014).

Among all vital processes, survival presents a more marked change as succession unfolds. In the initial years of the process, survival probability is close to 1 for all individual sizes, but in subsequent years this probability decreases rapidly, especially for smaller individuals. Lebrija-Trejos et al. (2011) described the environmental factors characteristic of the early stages of secondary succession, such as high soil and air temperatures, as well as low soil water availability. *Mimosa acantholoba* displays different functional attributes which confer it better performance under these conditions, such as high wood density, low wood water content, narrow leaves, small leaflets, and so forth (Romero et al., 2020a, 2020b). Within the guild of pioneer species encompassing few species that are capable of growing under these conditions (Lebrija-Trejos, Meave, et al., 2010; Lebrija-Trejos, Pérez-García, et al., 2010), *M. acantholoba* stands out as the only species commonly attaining large population sizes (Rozendaal et al., 2016), which is the case in our study. However, as these conditions continue to change in response to the structural community development, other species enter the community which appear to be better competitors for light (Dalmaso et al., 2020; Lebrija-Trejos et al., 2011; Saenz-Pedroza et al., 2020); ultimately,

this process of community taxonomic enrichment may be the major driver of the decrease in *M. acantholoba*'s survival, thus reducing population size. This possibility is supported by the fact that, at advanced successional ages, the survival probability decreased mainly for small-sized individuals, as observed elsewhere (Saenz-Pedroza et al., 2020). This can be related to a decrease in recruitment, since at this stage light availability has largely decreased in the understory (Lebrija-Trejos et al., 2011), causing a reduction in the production of resprouts and the establishment of newly recruited individuals (Maza-Villalobos et al., 2011). As succession unfolds, survival decreases even for medium to large sized organisms, supporting the idea that the mechanisms affecting survival are related to the height of individuals, so that competition for light could be a very relevant factor, as it is directly linked to this feature (Matsuo et al., 2021). Future analyses of light gradients through the canopies of this and other tropical dry forests may confirm this possibility.

Many pioneer species have high individual growth rates in the early years of succession (Galia Selaya et al., 2008). This growth, reflected in basal area increments, may be the main cause of the increase of biomass in pioneer species, even over fertility (Rozendaal & Chazdon, 2015). In some systems the growth rate decreases as succession advances, presumably due to changes in nutrient availability (Berger et al., 2006). However, in the case of *M. acantholoba*, the growth rate remained relatively constant with successional age, and it was higher for small individuals than for large ones (Figure 2b). This constant growth rate suggests that mechanisms potentially affecting the survival of individual trees, including decreased light availability, do not affect their growth. Regardless of the cause of the lack of variation in growth rates over time, individual growth does not appear to be responsible for the changes in basal area along succession; these changes could be rather explained by an increase in the number of individuals (Muñoz et al., 2021), which is consistent with the increase in individual density also observed. Thus, individual tree growth may be discarded as a major driver of population dynamics of *M. acantholoba* over succession.

Like other vital processes, fecundity was higher for larger individuals and decreased with successional age. Against initial expectations, seed production had very low values from the beginning and did not show an increase in early successional stages. Within the processes involving fecundity, the probability of establishment of individuals recruited from seed was particularly low, since the proportion of seeds that succeed to germinate and establish is extremely low (<0.0001). In other pioneer species this early stage of the life cycle has



already been identified as the bottleneck of their populations (Álvarez-Buylla & Martínez-Ramos, 1992; Martínez-Ramos et al., 2021), mainly due to decreased light availability in the understory (Maza-Villalobos et al., 2011). Thus, the effect of low fecundity added to a decreased survival gradually causes a reduction in population size, since more individuals die than establish. Other studies have found that resprouting in pioneer species may be a more important component of population maintenance than fecundity (Dietze & Clark, 2008). Therefore, due to its low values, we conclude that fecundity can hardly drive the population growth or biomass increase that occurs in *M. acantholoba* populations during the early phases of succession.

#### 4.2 | Successional patterns of *M. acantholoba*'s population attributes

The population size of *M. acantholoba* showed a pattern expected for a pioneer species, with high growth rates in the first years of succession, rapidly reaching its peak in the fourth year, and decreasing thereafter. However, the population size projected by the model presents much higher values than the observed maxima at the different plots. According to the projected model, the population begins to decrease very early in succession and becomes locally extinct around year 38. This contrasts with the observed data, since there are a few plots where a small population of late-stage individuals remains; however, these populations restrict to areas close to the hilltops, which present poorly developed soils that resemble early-successional sites.

The population growth rate also shows a general pattern that coincides with our expectations. At the onset of succession, the population growth rate attains its highest value, although the value projected by the model is higher than the observed one. It is possible that this general pattern is related to the probability of survival, the probability of establishment and resprouting, since these are the rates with the clearest responses to successional age, and changes in these processes coincide in time with the most important changes in the population level pattern. This seems to suggest that a large fraction of the changes in population dynamics, which occur in the first years of succession, are strongly determined by these three factors. Later, from the fourth year of succession onwards, the growth rate takes negative values. However, the values observed in different plots become very small before they take the values projected by the model. According to the model, after year 30 of succession, the population reduces its mortality and disappears at a slower rate, which is consistent with previous research

(Lebrija-Trejos, Meave, et al., 2010; Lebrija-Trejos, Pérez-García, et al., 2010).

Successional changes in population size structure occur before the most important changes in population size and growth rate have taken place. This implies the existence of a relatively short time-window, approximately between 10 and 30 years of successional age, in which practically all individuals attain their maximal sizes, between 5 and 7 m; thereafter, the population size structure remains relatively constant, regardless of the important changes in population dynamics that continue to occur.

#### 4.3 | Relevance of resprouting in the population dynamics of *M. acantholoba*

In various forest ecosystems, resprouting is an important component of biomass and individual production, with this process often being more important than production derived from recruitment from seeds (Bond & Midgley, 2001; Kennard, 2002; White, 1991). In particular, tropical dry forests have been suggested to have a higher share of species capable of resprouting than their moister counterparts (Bond & Midgley, 2001; Vieira & Scariot, 2006), where different types of disturbances, such as burning or even hurricanes, have been documented to have a positive effect on resprouting incidence (Dunphy et al., 2000; Kennard, 2002; van Bloem et al., 2007). Similarly, the population dynamics of *M. acantholoba* seems to be driven by resprouting, mainly over the first 5 years of succession. During this early successional period, individuals are not big enough to sustain sexual reproduction, but survival probability is very high, making resprouts very successful, in terms of height, basal diameter, cover and number of stems (Kennard, 2002). Thus, in this species, resprouting plays a major role in its dynamics in the early stages of succession.

However, the rapid decline in resprouting and the decrease in the probability of survival to later stages at the end of the succession and into the mature state of the forest, are the main drivers of the local extinction of *M. acantholoba*. This pattern is consistent with other studies showing an absence of resprouting in the mature forest (Kammesheidt, 1998; Rodrigues et al., 2004). It has been suggested that individuals derived from resprouting, having a multi-stemmed architecture, have a disadvantage in the competition for light with respect to single-stemmed individuals (Bellingham & Sparrow, 2000). This may explain why the population of *M. acantholoba* disappears almost completely before the end of the successional process, with only a handful of isolated individuals persisting in some patches of marginal mature forest.

Despite having a very similar resprouting probability to that of other species in the study site, *M. acantholoba* is the species with the highest absolute abundance of resprouts (Lebrija-Trejos, 2004). Under these conditions, it is reasonable to consider that the resprouting capacity of this species is one of the main factors in the dominance of this species, even more so than other demographic processes. Therefore, explicitly considering the resprouting ability helps better describe the dynamics of pioneer species such as *M. acantholoba*.

#### 4.4 | Methodological considerations

The experimental design in this study is based on the integration of two databases, which needs some consideration in interpreting the results of this work. We censused the plots from which we obtained the data used to model survival and growth from 2003 to 2016. In addition, for this study, it was necessary to gather data on the presence and number of reproductive structures in order to model fertility. These data had not been previously recorded, thus in 2017 we sampled these variables in the field. In that year, rains were recorded after several relatively dry years, possibly associated with ENSO (Muñoz et al., 2023). Therefore, it is important to note that the environmental conditions may have been very different between the two sets of data that fed the different models.

We carried out fruit counting and sampling in November, based on the phenological behavior of the species at the study site (Maldonado-Romo, 2014). During fieldwork, we observed ripe fruits and some fruits on the ground. Therefore, it is possible that the number of fruits counted may be an underestimation of the actual number produced, and thus underestimate  $f_2$ . No laboratory germination tests were done for this species and no studies are known to have done so, thus the conversion factor from seeds to seedlings was calculated using inverse estimation (González et al., 2016). Very likely, the inclusion of an in situ germination study would produce better germination estimates; however, inverse estimation is a good approach in the absence of such studies.

Similarly, it is important to keep in mind that the database used to model growth and survival is much larger than that for fecundity, making it more difficult to identify outliers in fecundity. Therefore, we cannot rule out that the low values observed in fecundity may be related to all of the above. In order to better understand reproduction, it is important to have a larger database and to consider different years of sampling in order to have greater control over interannual variation.

## 5 | CONCLUSIONS

Although there are many factors shaping the population dynamics of *M. acantholoba* var. *eurycarpa*, the initial one given by its high resprouting ability seems to be the most relevant demographic component. The ecological characteristics of this species, such as low growth rate and low fecundity, do not allow it to undergo demographic processes that maintain a stable population through the entire duration of a secondary successional process, estimated to last in the study forest more than a century. This combination of factors results in this species being restricted to early and young stages of succession or to disturbed sites. Therefore, resprouting should be explicitly considered when understanding the population dynamics of pioneer species having this capacity, especially in tropical dry forests facing disturbance.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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