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Original Research Article

# Unexpected spatial patterns of natural regeneration in typical uneven-aged mixed pine-oak forests in the Sierra Madre Occidental, Mexico



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## ABSTRACT

Natural forest regeneration, i.e. self-renewal of forest stands, involves the replacement of old trees by the next generation and is influenced by environmental factors. The spatial structure of tree regeneration depends on and also influences the properties of the stands themselves. Few studies have investigated spatial patterns of naturally regenerated areas in Mexican pine–oak forests, which are considered one of the world's top 34 biodiversity hotspots. In this study, we analyzed the spatial patterns, particularly the spatial structure, in clusters of naturally regenerated trees in seven 100 × 100 m plots in the Sierra Madre Occidental (northern Mexico), in relation to three factors: slope, geographical aspect and distance between each sapling to the edge of the nearest gap in the canopy. Three indices were used to describe spatial structure and the data were analyzed by bivariate Ripley's *K*(*t*)-functions and three-parameter and six-parameter Weibull models. The results indicate that sapling regeneration was marginal in canopy gaps. Sapling density was ten times higher under the canopy cover, close to the edge than in the gaps. On average, the first maximum number of saplings was detected inside the canopy at about 81 cm from the gap edge, forming ring-type spatial patterns around the canopy gaps. These results contrast with the gap dynamics described in many other studies. We attribute these findings to the nurse effect of trees, which ameliorate abiotic effects, such as the extreme drought that occurred in 2011 and 2012 in the study region. In covered zones close to canopy edges, these orientation. We recommend adapting or changing the current forest management system to improve continuous forest regeneration (including adaptive silviculture). We also strongly support i) research on the effects of cattle grazing on natural regeneration in the region and ii) reduction of livestock pressure, which is essential to support forest renewal. Complementary reforestation, in addition to maintenance of the few saplings growing within the gaps, may help enhance forest regeneration. Finally, the use of

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alternative regeneration methods, such as an irregular group shelterwood method (Expanding Gap Silviculture “Femelschlag”), should also be considered, in order to promote natural regeneration more purposefully.

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## 1. Introduction

The Sierra Madre Occidental (SMO) occupies about 29 million hectares (Silva-Flores et al., 2014), within which pine–oak and other temperate forests cover an area of more than 19 million hectares (González-Elizondo et al., 2012). These forests are classified as Nearctic subtropical coniferous forests (Ricketts et al., 1999). This area is considered one of the world’s top 34 biodiversity hotspots (Mittermeier et al., 2011), since these forests harbour a high diversity of flora, including 24 pine species (ca. 22% of the world’s total), 54 oak species (ca. 9–14%), seven species of *Arbutus* (more than 50%) and many other tree species (González-Elizondo et al., 2012, 2013; Silva-Flores et al., 2014). They are typically mixed uneven-aged forests and are selectively managed, mainly by groups of owners of local communities known as ejidos (Thoms and Betters, 1998; Wehenkel et al., 2011).

Those forest areas could be managed under optimal continuous-cover forest (CCF) systems, where the stand characteristics should oscillate around some optimal levels of standing growing stock, forest diversity or structure, in order to enable maximization of net benefits through periodic harvesting of the volume growth (Hyytiäinen and Haight, 2012; Gadow et al., 2012). However, these three important ideal growing stock traits and strategies seem to have been widely ignored and have not been studied in the SMO areas, making questionable the sustainability of those forests (Wehenkel et al., 2014).

Forest structure is a central feature in the CCF management system, as it defines the current potential output of products and services, as well as the resilience and future dynamics of the managed ecosystem (Pommerening and Murphy, 2004; Schütz et al., 2012). Moreover, analysis of forest structure can help to determine the functionality and detect the main disturbances in forest ecosystems (Spies, 1998; Pommerening, 2006), as well as to unravel the complex biological process of natural forest regeneration (Park, 2001).

The replacement of old trees, through natural forest regeneration, depends on environmental conditions (Fischer et al., 2016). The structure, composition and function of natural forest stands depend on the forest dynamics, beginning with the establishment of tree regeneration (Franklin et al., 2002). The spatial structure of tree regeneration (including seedlings and saplings distribution) is an important component of forest structure, because of its influence on the properties of the system, including total biomass production, biodiversity and habitat functions, as well as the quality of ecosystem services. As with the structure of other forest components, the structure of the juvenile stages of the trees refers to patterns of attributes, including structural type, size, shape and spatial distribution (vertical and horizontal) (Spies, 1998; Gadow et al., 2012). Naturally regenerated juvenile trees are not usually uniformly distributed, as they typically grow together (in groups) or are randomly distributed (Clark and Evans, 1954; Ripley, 1977; Lepš and Kindlmann, 1987).

In managed uneven-aged pine–oak stands in the SMO, these juvenile trees are usually situated in small canopy gaps, scattered throughout the stand (Wehenkel et al., 2011). These forest gaps can be caused by natural disturbances and also by the harvesting of the largest trees for timber. The silvicultural system based on CCF management is known in Mexico as the *Método Mexicano de Ordenación de Bosques Irregulares* (MMOBI) (Rodríguez, 1958; Torres, 2000) and is based on natural regeneration and gap dynamics (Yamamoto, 2000). Runkle (1981) defined two types of gaps: “canopy gaps”, the areas directly under canopy openings, and “expanded gaps”, the canopy gaps plus the adjacent area up to the stem bases of the canopy trees bordering the gap, including areas directly and indirectly affected by the canopy opening.

Few studies have investigated spatial patterns of naturally regenerated areas in Mexican pine–oak forests (Chacón-Sotelo et al., 1998; Park, 2001; Reyna et al., 2019), which cover an area of 31.8 million hectares (FAO, 1998). In this study, we analyzed the spatial patterns and particularly the type of spatial structure of clusters of naturally regenerated trees, in seven 100 × 100 m plots, in relation to three factors: slope, geographical aspect and distance between each sapling and the edge of the nearest gap in the canopy. Our overall aim was to identify the environmental factors and forest community structure properties that influence the recruitment of naturally regenerated saplings under the canopy cover and inside forest gaps, in typical temperate forests in the northern region of the Sierra Madre Occidental, Mexico.

As these forests are commonly uneven-aged and mixed pine–oak stands (Wehenkel et al., 2011), we hypothesized that the regenerated juvenile trees will almost always be located in groups within the gaps in the canopy (Runkle, 1981; Shugart, 1984; Whitmore, 1989; Muscolo et al., 2014; Cañadas et al., 2018) and that species-specific differences will occur (van der Maarel, 1988; Yamamoto, 2000; Muscolo et al., 2014). We also anticipated natural forest regeneration to be more abundant in gently sloping areas, where drainage is adequate, soil erosion is often minimal and soil conditions are therefore better (e.g. deeper soils and higher concentrations of available and exchangeable nutrients) (Tsui et al., 2004; Guerra et al., 2017). Finally, we assumed that natural regeneration will preferentially occur on northerly slopes, which are moister than southerly slopes as they are shaded for longer periods during the day in the northern hemisphere (Brooks and Merenlender, 2001).

## 2. Methods

### 2.1. Study area

The study area is located in the Sierra Madre Occidental, in the municipality of Madera, northwest of the state of Chihuahua, Mexico (Fig. 1). The area (geographical coordinates 28° 41' 18" to 30° 0' 14" N and 107° 47' 06" to 108° 45' 13" W) lies within the Regional Forest Management Unit (UMAFOR) 0802, which consists of about one million hectares of forest. Pine-oak temperate forest is the most important vegetation type and is dominated by *Pinus arizonica* Engelm., *P. durangensis* Martínez, *P. engelmannii* Carr., *P. leiophylla* Schltdl. & Cham., *P. strobiformis* Engelm., *Arbutus xalapensis* Kunth s.l., *Juniperus deppeana* Steud., *Quercus sideroxyla* Humb. & Bonpl. and *Q. arizonica* Sarg. The annual average temperature ranges from 9.3 to 11.1 °C; precipitation ranges between 650 and 969 mm, and the soil pH ranges from 5.4 to 6.1 (Wehenkel, 2016). The climate station in

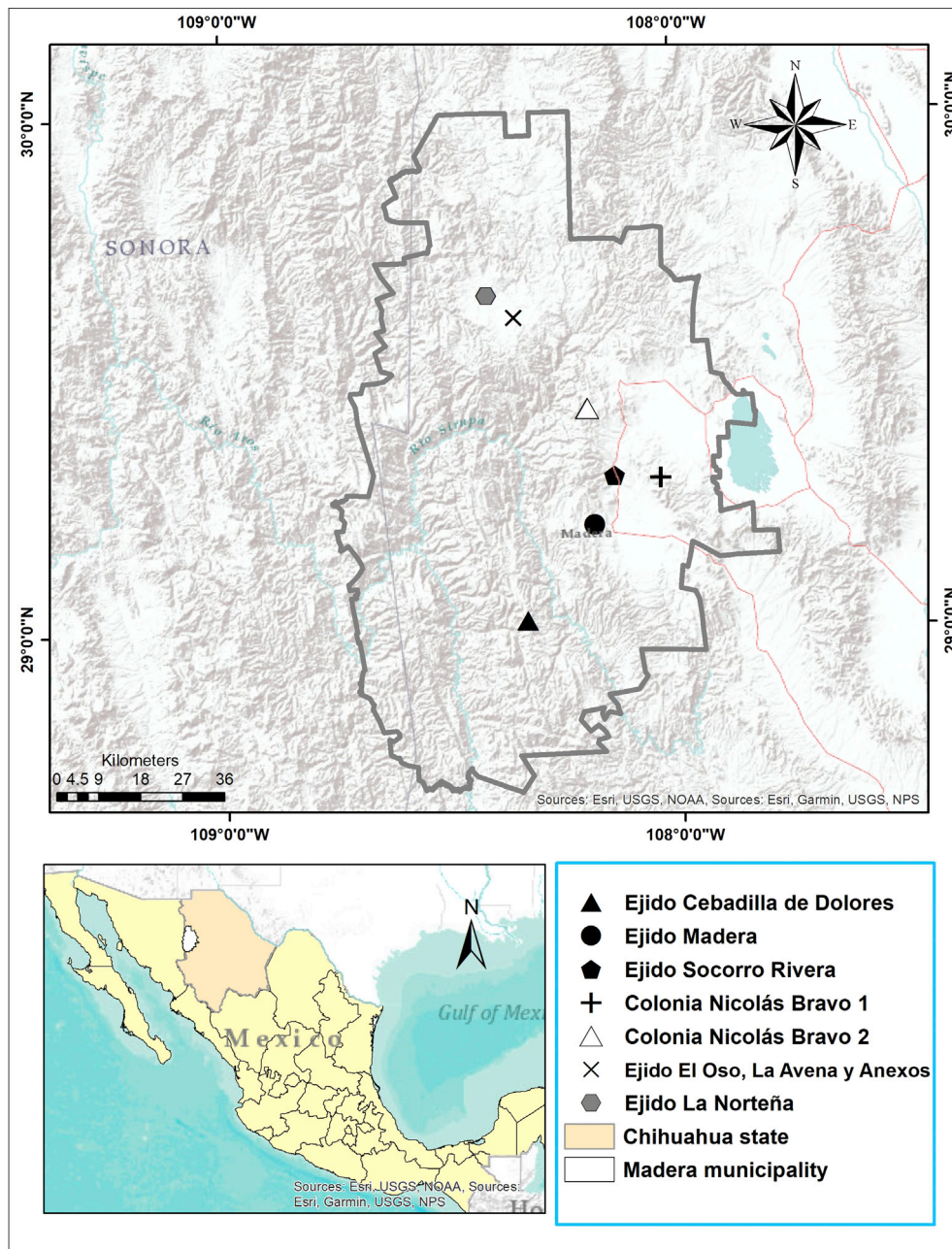


Fig. 1. Locations of the seven study sites represented by 100 × 100 m (1 ha) plots, which were randomly distributed in six previously selected forest communities.

Mesa del Huracán, Madera, Chih., (located in the northern part of the study area) registered a mean precipitation of 649 mm (minimum 489 mm, maximum 929 mm) in the period 1998–2017 (Fig. S1).

## 2.2. Sampling sites and variables

The sampling design included seven study sites, each represented by a plot of  $100 \times 100$  m (1 ha) (Manzanilla, 1993) (divided into  $50 \times 50$  m subplots), which were randomly distributed in six previously selected forest communities (five "ejidos" and one "colonia") (Fig. 1). In each study site, saplings and trees of all species, of diameter at breast height (DBH)  $\geq 1$  cm, were fully scored. The DBH, height, crown diameter and coordinates (X and Y) were also recorded. The crown diameter was measured on the north-south axis and again on the east-west axis. The number of stems per hectare ( $N$ , stems/ha), stand basal area ( $G$ ,  $m^2/ha$ ), mean diameter at the breast height ( $DBH$ , cm), mean total height ( $H$ , m), maximum diameter ( $D_{max}$ , cm) and maximum height ( $H_{max}$ , m) were computed for each plot. The stand volume ( $V$ ,  $m^3/ha$ ) of the plot was estimated using the diameter and height values for each tree and one regional volume model (Simental-Cano et al., 2017, Table 1). The diameter structures of the seven studied plots and of the tree species are shown in Fig. 2a and b and Figs. S2 and S3.

In order to test the hypothesis, we also considered the following variables for each sapling: trees belonging to the understorey with DBH below 7.5 cm, according to CONAFOR (2015); this is often considered as limitation between sapling stage and adulthood (e.g., Lundqvist, 1994; Camarero and Gutiérrez, 2002; Barbeito-Sánchez, 2009; Kerr and Mackintosh, 2012), slope (SLO, percent), geographical aspect (ASP, azimuth) and distance to the edge of the nearest gap in the canopy (DIS, cm). All canopy gaps with a minimum average width of 4 m (i.e. minimum area of  $16 m^2$ ), delimited by the outline of the crowns of upperstorey trees with DBH  $\geq 7.5$  cm (Runkle, 1981; CONAFOR, 2015), were also recorded (Figs. S4 and S5). While Liu and Hytteborn (1991) studied gaps with minimum size of  $9 m^2$  and Hubbell et al. (1999) gap sizes of  $25 m^2$ , we recorded gaps with a minimum area of  $16 m^2$ , which we considered valid for inclusion in the study as tree seedlings successfully emerge and saplings grew within them (especially in areas adjacent to the expanded gaps) (Table 1).

The distribution of the gap sizes corresponded to a power function, and 69% of the 231 gaps were smaller than  $100 m^2$  (Fig. S6). The limits of expanded gaps (consisting of the canopy gap plus the adjacent area extended to the stem bases of the canopy trees bordering the gap) were also recorded. In each expanded gap, the position of each tree relative to the edge of the canopy gap (crown outline) was also recorded.

In each expanded gap, all saplings at a maximum distance of 2 m from the nearest edge of the canopy gap (crown outline) were recorded. The distance (cm) from each sapling found, either inside the canopy cover or inside a gap, to the edge of the canopy gap (crown outline) was then measured using ArcMap (Version 10.0, ArcGIS) (ESRI, 2012). The distance from each sapling found inside the canopy cover to the stem bases of canopy trees bordering the gap was also registered. To determine distance (class), 20 buffer areas (10-cm width each, from 0 to 2 m) surrounding each gap edge were established using the buffer tool in ArcMap (ESRI, 2012) (Fig. S7). Table S1 lists the number and density of tree saplings under the canopy cover, at the edge of the canopy gaps and inside the gaps, for each sampling plot and tree species. The mean crown radius of the upperstorey trees ( $\geq 7.5$  cm DBH) growing at the edges of gaps was 1.58 m (1.39–2.01 m, depending on the plot; 1.40–1.93 m, depending on the tree species).

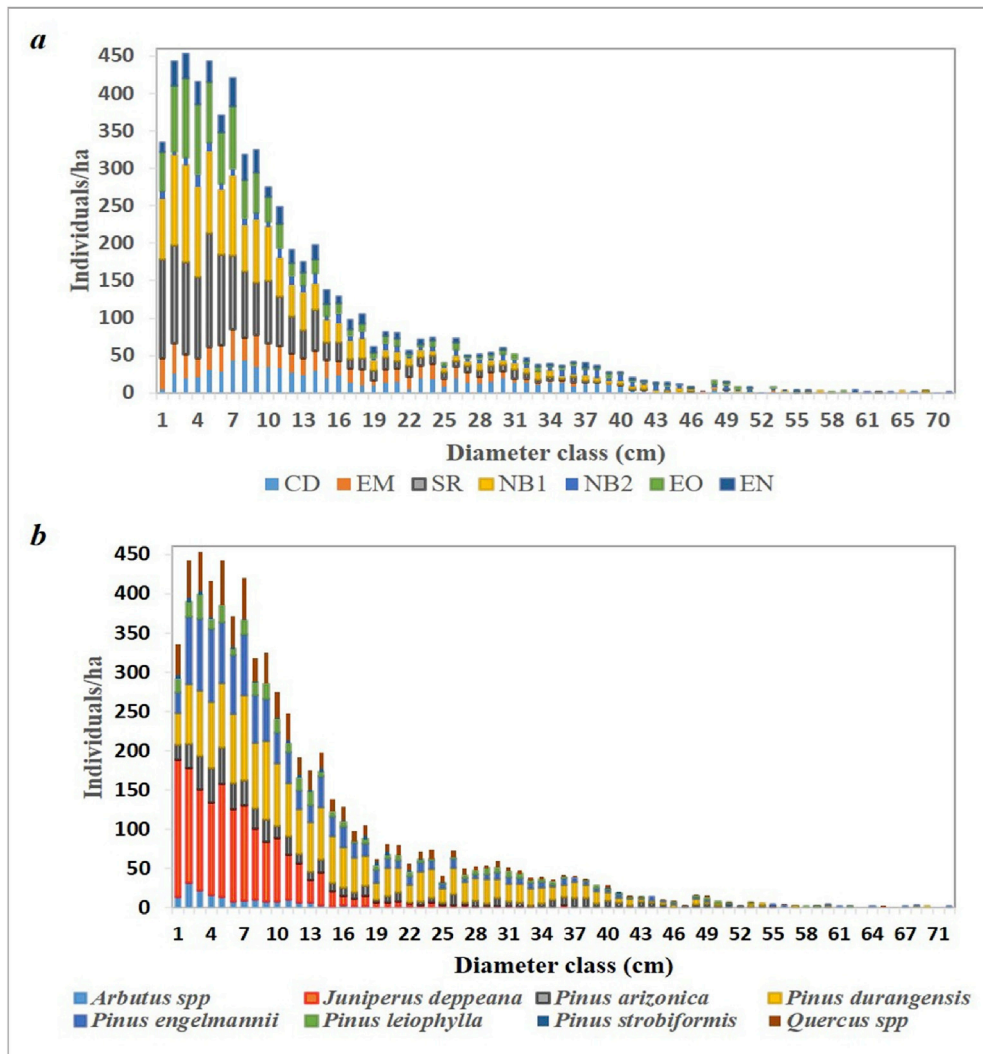
Finally, in order to check differences in soil properties between the canopy cover and the gaps, 23 soil characteristics (Table S2) were determined in four samples per plot (28 samples, each taken at the centre of the  $50 \times 50$  m subplots) by using the soil analysis method described by Wehenkel et al. (2015). A total of 15 soil samples were obtained from the area under the canopy cover and 13 from the gaps.

**Table 1**

Geographical coordinates and summary of the climate, soil and stand variables calculated from the tree data: stand basal area ( $G$ ) per hectare, mean breast height diameter (DBH), mean total height ( $H$ ), maximum diameter ( $D_{max}$ ), maximum height ( $H_{max}$ ) and stand volume ( $V$ ) in the  $100 \times 100$  m plots in the seven study locations. MAT = mean annual temperature ( $^{\circ}C$ ), MAP = mean annual precipitation (mm).

Plot	Code	Geographical coordinates	MAT ( $^{\circ}C$ )	MAP (mm)	pH	DBH (cm)	H (m)	$D_{max}$ (cm)	$H_{max}$ (m)	$G$ ( $m^2/ha$ )	$V$ ( $m^3/ha$ )
Ejido Cebadilla de Dolores	CD	29°01'11.50"N, 108°20'09.58"W	9.7	969	5.80	17.9	11.4	70	28	26.5	257
Ejido Madera	EM	29°12'15.92"N, 108°11'04.20"W	9.7	827	5.68	14.5	7.7	68	25	19.5	143
Ejido La Norña	EN	29°39'04.50"N, 108°24'51.70"W	10.9	821	5.55	13.1	6.5	72	30	11.9	103
Ejido El Oso, La Avena y Anexos	EO	29°36'29.40"N, 108°21'15.50"W	10.7	801	5.72	10.2	5.9	59	25	15.8	124
Colonia Nicolás Bravo 1	NB1	29°17'36.80"W, 108°02'12.40"W	9.8	762	5.70	10.4	5.3	69	22	22.3	142
Colonia Nicolás Bravo 2	NB2	29°25'46.60"N, 108°11.0'42.2"W	9.3	849	5.59	23.0	13.1	60	29	22.8	264
Ejido Socorro Rivera	SR	29°17'54.57"N, 108°08'21.0"W	11.1	650	5.63	9.5	5.1	68	23	19.8	106
<b>Mean</b>			10.2	811	5.70	14.1	7.9	67	26	19.8	163





**Fig. 2.** a) Diameter distributions in the seven 100 × 100 m forest plots; b) Diameter distributions for the studied tree species. Ejido Cebadilla de Dolores (CD), Ejido Madera (EM), Ejido La Norteña (EN), Ejido El Oso, La Avena y Anexos (EO), Colonia Nicolás Bravo 1 (NB1), Colonia Nicolás Bravo 2 (NB2) and Ejido Socorro Rivera (SR).

### 2.3. Data analysis

#### 2.3.1. Analysis of spatial structure

The Clark-Evans index ( $CE$ ) (Clark and Evans, 1954) and the Uniform Angle index ( $\bar{W}$ ) (Gadow et al., 1998) were used to describe the spatial structure of the naturally regenerated saplings in each study plot, on the basis of the spatial distribution of the  $n$  saplings nearest to a reference sapling  $i$ . The  $\bar{W}$  was computed for four neighbouring saplings ( $n = 4$ ), while  $CE$  was estimated for the nearest neighbouring sapling ( $n = 1$ ) (Albert, 1999; Hui and Hu, 2001; Wehenkel et al., 2015), by using the following expression:

$$CE = \frac{1}{N} = \frac{\frac{1}{N} \sum_{i=1}^N r_i}{0.5 \left( \frac{A}{N} \right)^{1/2}} \quad [1]$$

where  $N$  is the total number of saplings in the sample plot,  $A$  is the area of the plot (in  $m^2$ ) and  $r_i$  is the distance between sapling  $i$  and its nearest neighbouring sapling (in  $m$ ). A Poisson (random) distribution pattern was distinguished by a  $CE$  value of 1, aggregation trend by  $CE < 1$  and a trend to regular distribution of sapling by  $CE > 1$ , with a maximum of 2.1491 for a hexagonal configuration of the saplings.

In order to calculate  $\bar{W}$ ,  $W_i$  was first computed, as follows:

$$W_i = \frac{1}{n} \sum_{j=1}^n v_{ij} \text{ with } v_{ij} = \begin{cases} 1, & \alpha_{ij} < \alpha_0 \\ 0, & \text{otherwise,} \end{cases} \quad [2]$$

where  $\alpha_{ij}$  corresponds to the smallest angle between trees  $i$  and  $j$  ( $\alpha_{ij}$  has  $180^\circ$  as maximum value). The angle  $\alpha_0$  was set at  $72^\circ$ , which yielded a mean value of  $\bar{W} = 0.5$  (Hui and Gadow, 2002). For each sapling, the value of  $W_i$  was determined and the average  $\bar{W}$  for all saplings was then calculated.  $W_i$  and  $\bar{W}$  values close to 0 were associated with a regularly distributed neighbourhood of saplings, while values of  $W_i$  and  $\bar{W}$  close to 1 corresponded to an irregular neighbourhood of saplings. To exclude the impact of the edge effect on  $CE$  and  $\bar{W}$ , and therefore to enhance the accuracy of the estimates, we used the nearest-neighbour edge-correction concept (Pommerening and Stoyan, 2006).

### 2.3.2. Spatial structural analysis by univariate and bivariate Ripley's $K(t)$ -functions

The univariate Ripley's  $K(t)$ -function was used to identify the scales at which the sapling pattern in each plot tends to be clustered, random or regular. The  $K(t)$ -function was normalized using the  $L$ -function proposed by Besag (1977). The expected value of the univariate  $L$ -function ( $L(r)$ ) under complete spatial randomness (CSR) is 0 for all distances ( $r$ ) from an arbitrarily selected point (sapling) of the study region (plot), positive ( $L(r) > 0$ ) when the pattern tends to be clumped and negative when the pattern tends to be regular ( $L(r) < 0$ ).

The bivariate  $K$ -function (Dixon, 2002) was used to describe the relationship between the saplings spatial pattern and the spatial structure of upperstorey trees within the seven plots. The expected value of the bivariate  $L$ -function ( $L_{12}(r)$ ) under spatial independence, is 0 for all  $r$ , i.e. the spatial patterns of saplings and upperstorey trees are independent when  $L_{12}(r) = 0$ . The value is positive ( $L_{12}(r) > 0$ ) when the patterns for saplings and upperstorey trees tend to be aggregated and negative when repulsive patterns of the saplings to the upperstorey trees are observed ( $L_{12}(r) < 0$ ).

In order to test the statistical deviation from independence for both patterns ( $L(r)$  and  $L_{12}(r) = 0$ ), the 99% confidence interval of  $L(r)$  and  $L_{12}(r)$  was computed using the Monte Carlo method and 1,000 simulated CSR patterns (Besag, 1977; Besag and Diggle, 1977) (for details, see Wehenkel et al., 2015).

### 2.3.3. Influence of slope, geographical aspect, distance to the edge of the canopy covered areas and soil properties on the spatial distribution of natural regeneration

The following procedure was carried out when spatial clustering tendencies and differences in the density of natural regeneration between canopy cover and canopy gaps were detected. The association between the mean number of saplings and the distance from each sapling to the edge/border of canopy cover (here considering only the saplings found within the first 2 m under the canopy cover) was determined (along with the topographical location/position, i.e. slope and geographical aspect of the areas) using three (W3p) and six-parameter Weibull (W6p) models, executed in "FADist" and the "carditates" software packages (Petzoldt et al., 2007; Rolinski et al., 2007a, 2013) implemented in the free statistical application R (R Development Core Team, 2017). For each slope and geographical aspect, the size of the canopy cover was different in the seven plots, and these variables were therefore compared in terms of number of saplings per hectare in each plot.

The W3p distribution (Weibull, 1951) and its extended forms are very popular, robust and flexible models. The W3p is characterized by its shape, scale and location parameters (Murthy et al., 2004; Yousof et al., 2017). However, the W3p distribution is not robust for modelling phenomena with non-monotone failure rate (Mudholkar and Srivastava, 1993).

Nonetheless, W3p can be extended to a six-parameter model (W6p):

$$w(x) = \left(1 + p_1 \exp\left(-\left(\frac{x}{p_2}\right)^{p_3}\right)\right) \times \left(p_4 + \exp\left(-\left(\frac{x}{p_5}\right)^{p_6}\right)\right) \quad [3]$$

where  $w(x)$  is the probability distribution of an  $x$  independent variable (saplings number) and  $p_1 \dots p_6$  are the parameters to be fitted.  $p_1$  equals the offset after the peak,  $p_2$  and  $p_3$  are the inflexion point and the steepness of the decreasing branch, respectively.  $p_4$  determines the offset before increase (offset =  $(p_1 + 1) * (1 - p_4)$ ),  $p_5$  and  $p_6$  are the inflexion point and the steepness of the increasing branch.

The function allows for different slopes in the increasing and declining sections as well as non-zero baselines before and after the peak (Rolinski et al., 2007b). W6p is therefore often more robust than Wp3 for capturing the slope change in the tail distribution and predicts extreme statistics more reliably (Izadparast and Niedzwecki, 2013). However, a smaller number of parameters (not affecting the suitability of the model) is mathematically more appealing (Glänzel and Hamedani, 2001).

A well-fitting model results in predicted values close to the observed values, detected by a high Pearson coefficient of determination ( $R^2$ ) and a small probability value ( $p$  value) (Sokal and Rohlf, 1995; Mesplé et al., 1996). A model is considered acceptable when its  $p$  value is smaller than 0.0046 (after Bonferroni correction). The best-fitting regression model is that with the lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC), which are measures of the compromise between maximizing the goodness of fit and minimizing the number of parameters (Akaike, 1974; Rolinski et al., 2007b).

For W6p, the "cardinal" numbers of saplings, corresponding to the beginning, maximum and end of changes (and trends) in the distribution of the number of saplings, were determined using the method of Rolinski et al. (2007b). This method is based on nonlinear regression of a function  $w(x)$  (Eq. (1)) and requires linear interpolation between values in some cases. It is

recommended when very few observations precede the peak, i.e. when fewer than 5 values are above the mean value. The fitted function  $w(x)$  is used to determine these cardinal numbers. The maximum value of  $w(x)$  corresponds to the “maximum” cardinal number of saplings. Thus, the area under  $w$  was computed as the integral of the number of saplings before and after the  $w$  peak, separately. The cardinal sapling number denoted “outbreak” represents the number of saplings in the 10% quantile of the area before the  $w$  peak (maximum) and the cardinal sapling number, denoted “collapse”, represents the number of saplings in the 90% quantile of the area after the peak (Rolinski et al., 2007b).

Finally, possible differences in saplings density (sapling number ( $N$ ) per area,  $N/m^2$  or  $N/ha$ ) and in 23 soil properties between the canopy covered areas and the canopy gaps were examined using a non-parametric Kruskal-Wallis test (Kruskal and Wallis, 1952) ( $\alpha = 0.002$  after Bonferroni correction).

### 3. Results

#### 3.1. Analysis of spatial structure

In all seven plots studied, the saplings tended to grow in clusters, as confirmed by the Clark-Evans index ( $CE$ ) and the uniform angle index ( $\bar{W}$ ), as the mean  $CE$  value was always less than one, and  $\bar{W}$  was always greater than 0.5 (Table 2). In each studied plot, moreover, the univariate  $L$ -functions ( $L(r)$ ) showed significant aggregation tendencies at  $r$  from 0 to 20 m (Fig. 3a and Fig. S8a).

In all studied plots, the bivariate  $L$ -function ( $L_{12}(r)$ ) demonstrated a significant tendency for saplings (DBH below 7.5 cm) and upperstory trees ( $\geq 7.5$  cm DBH) to grow together (Fig. 3b and Fig. S8b). The spatial distribution pattern of saplings of each species was also quite similar to the spatial distribution pattern of the saplings of all the tree species together.

The mean sapling density was 393 individuals per ha (43% of saplings and upperstory trees together). The species composition of saplings was very similar to the species composition of upperstory trees (Table S1). In all plots, the mean sapling density under the canopy (0.06 saplings per  $m^2$ ) was significantly higher than in the canopy gaps (0.006 saplings per  $m^2$ ) (Table 2), as confirmed by the Kruskal-Wallis test ( $p = 0.0017$ ). None of the soil properties measured in all study plots in this study differed significantly between the canopy covered areas and the canopy gaps.

#### 3.2. Influence of slope, geographical aspect, distance from the edge of the canopy and soil properties on the spatial distribution of natural regeneration

The number of saplings that grew between the stem bases of canopy trees bordering the gap and the canopy edge, within a maximum distance of 2 m from that edge, depended significantly on the distance from the canopy edge, slope and geographical aspect. Within this interval, and depending on the tree species, the modelled maximum number of saplings was found to be in the range of the 60–107 cm closest to the canopy edge (i.e. to the crown edge of adjacent upperstory trees, estimated from fitted curves from the six-parameter Weibull model (W6p) (Table 3).

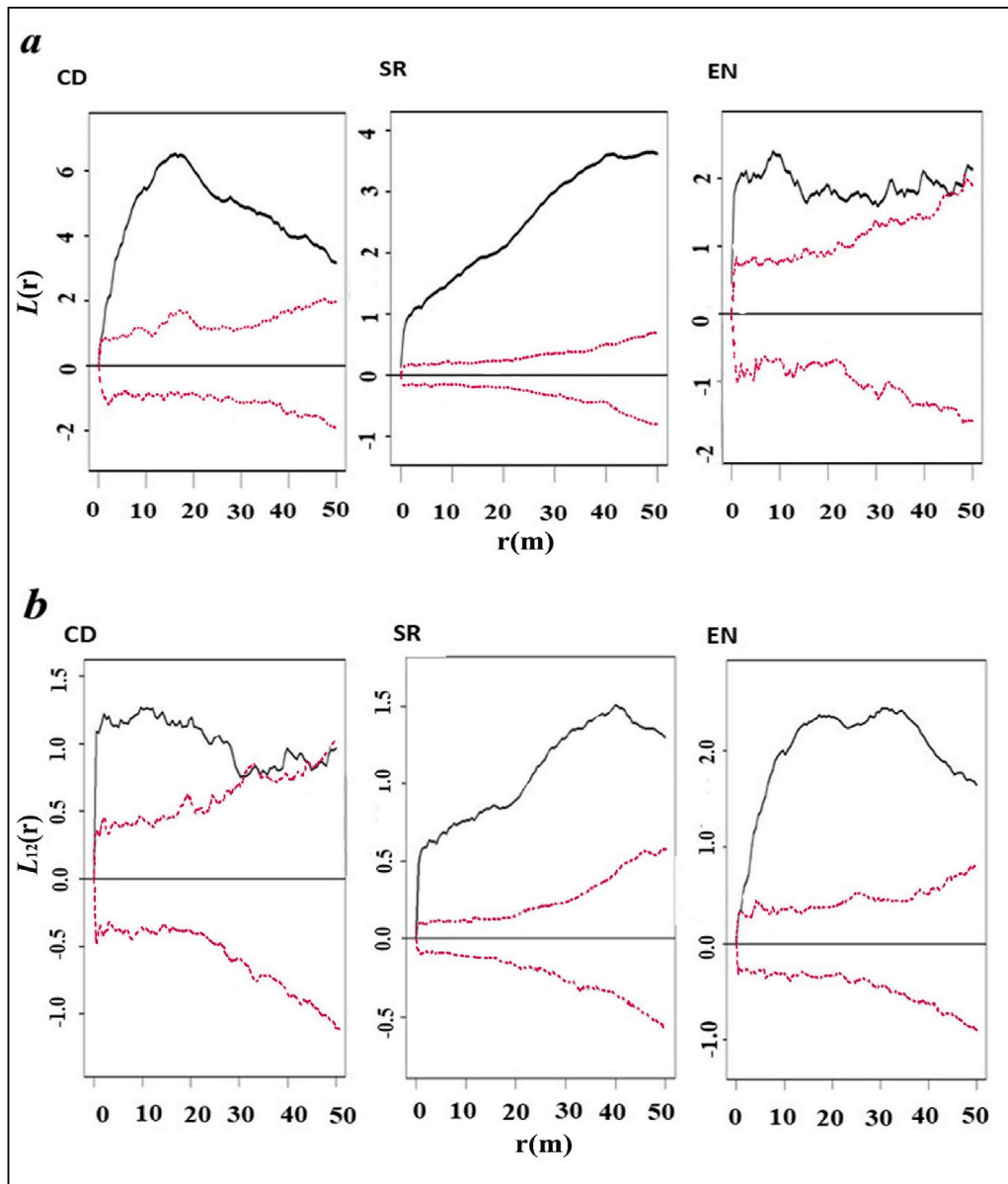
Regarding all of the tree species between the stem bases of canopy trees bordering the gap and the canopy edge (among all plots), the modelled mean number of saplings was notably greater at a distance of 44 cm from the canopy edge, reaching a maximum number of about 160 saplings at the distance of 81 cm from the canopy edge and then decreasing until a distance of 147 cm (Fig. 4). Finally, in the distance class of 145–205 cm from the edge of the canopy cover (which is also the gap edge), the modelled mean number of saplings of all species studied remained relatively constant, at about 50 saplings. The maximum

**Table 2**

Results of the spatial structure analysis of the natural regenerated saplings (i.e. all saplings with DBH <7.5 cm) in each study plot, on the basis of mean Clark-Evans index ( $CE$ ) and Uniform angle index ( $\bar{W}$ ). SD = standard deviation.

Plot	$CE$	$\bar{W}$
<b>CD</b>	0.679	0.563
<b>EM</b>	0.564	0.595
<b>EN</b>	0.615	0.572
<b>EO</b>	0.713	0.529
<b>NB1</b>	0.722	0.509
<b>NB2</b>	0.497	0.597
<b>SR</b>	0.742	0.560
<b>mean</b>	0.647	0.561
<b>max</b>	0.742	0.597
<b>min</b>	0.497	0.509
<b>SD</b>	0.092	0.032

Plots: Ejido Cebadilla de Dolores (CD), Ejido Madera (EM), Ejido La Norteña (EN), Ejido El Oso, La Avena y Anexos (EO), Colonia Nicolás Bravo 1 (NB1), Colonia Nicolás Bravo 2 (NB2) and Ejido Socorro Rivera (SR).



**Fig. 3.** a) Spatial patterns of saplings represented by univariate  $L$ -functions. b) Relationship between spatial patterns of saplings vs. adult trees in three  $100 \times 100$  m study plots. The univariate ( $L(r)$ ) and bivariate ( $L_{12}(r)$ )  $L$ -functions are represented by black lines and the 99% simulation envelope for complete spatial random (CSR) hypothesis, by dashed red lines. The simulation envelope was computed by Monte Carlo method with 1,000 simulations. The expected value of the  $L$ -functions under CSR is 0 for all distances ( $r$ ) from an arbitrarily selected sapling of the study region (plot): Ejido Cebadilla de Dolores (CD), Ejido Socorro Rivera (SR), Ejido La Norteña (EN). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

number of saplings was found at a modelled mean distance of 77 cm from the tree stem bases to the edge of the gap (65–103 cm, depending on tree species) (Fig. 4).

The maximum number of saplings of *Arbutus* spp., *Quercus* spp. and *Pinus strobiformis* were projected on slopes of about 4, 10 and 19° respectively. The median values of these three distributions were significantly different ( $p < 10^{-10}$ ). The maximum number of saplings of *Arbutus* spp., *Pinus engelmannii*, *Quercus* spp., *Pinus strobiformis*, *Pinus leiophylla*, and *Pinus durangensis* were predicted to occur on north-western geographical aspects (by significant W6p models). However, the median numbers of saplings per hectare were not significantly different in relation to aspects. Among all the species studied, the maximum number of saplings (per ha) was expected for an aspect of 282° (Fig. 4, Table 3).

The W6p models were more robust and provided more reliable predictions of the spatial sapling distribution than the W3p models in relation to the distance between the sapling location and the edge of the nearest canopy gap, slope and geographical aspect, as indicated by lower absolute AIC and BIC values (Fig. 4, Table 4 and Table S3). However, only about 87%



**Table 3**

Cardinal numbers of saplings estimated from fitted curves corresponding to the start of the slope/rise of the curve (outbreak), curve maximum (max) or peak and the end of the slope/decrease of the curve (collapse), used to model the horizontal distribution of saplings vs. the distance from the edge of the canopy cover, slope and geographical aspect (under the canopy within a maximum distance of 2 m from the edge of the canopy).

<b>Cardinal number of saplings</b>			
<b>Variable</b>	<b>outbreak</b>	<b>max</b>	<b>collapse</b>
<b>Distance (cm) to the gap edge</b>			
<i>Arbutus</i> spp.	59.7	61.5	263.4
<i>Juniperus deppeana</i>	<b>55.8</b>	<b>74.4</b>	<b>167.1</b>
<i>Pinus arizonica</i>	<b>44.8</b>	<b>64.5</b>	<b>156.6</b>
<i>Pinus durangensis</i>	<b>51.4</b>	<b>81.1</b>	<b>143.7</b>
<i>Pinus engelmannii</i>	<b>33.5</b>	<b>79.1</b>	<b>120.1</b>
<i>Pinus leiophylla</i>	55.8	62.4	93.9
<i>Pinus strobiformis</i>	<b>103.5</b>	<b>107.1</b>	<b>115.1</b>
<i>Quercus</i> spp.	<b>58.3</b>	<b>86.6</b>	<b>128.9</b>
Total	<b>44.2</b>	<b>81.3</b>	<b>147.4</b>
<b>Slope (°)</b>			
<i>Arbutus</i> spp.	<b>3.6</b>	<b>3.9</b>	<b>13.6</b>
<i>Juniperus deppeana</i>	n. a.	n. a.	n. a.
<i>Pinus arizonica</i>	15.5	16.0	16.7
<i>Pinus durangensis</i>	n. a.	n. a.	n. a.
<i>Pinus engelmannii</i>	n. a.	n. a.	n. a.
<i>Pinus leiophylla</i>	n. a.	n. a.	n. a.
<i>Pinus strobiformis</i>	<b>18.5</b>	<b>18.7</b>	<b>n. a.</b>
<i>Quercus</i> spp.	<b>5.3</b>	<b>10.2</b>	<b>11.2</b>
Total	n. a.	n. a.	n. a.
<b>Geographical Aspect (0–359°)</b>			
<i>Arbutus</i> spp.	<b>243</b>	<b>267</b>	<b>304</b>
<i>Juniperus deppeana</i>	115	310	363
<i>Pinus arizonica</i>	54	178	297
<i>Pinus durangensis</i>	<b>273</b>	<b>297</b>	<b>312</b>
<i>Pinus engelmannii</i>	<b>262</b>	<b>277</b>	<b>297</b>
<i>Pinus leiophylla</i>	<b>268</b>	<b>294</b>	<b>307</b>
<i>Pinus strobiformis</i>	<b>282</b>	<b>293</b>	<b>308</b>
<i>Quercus</i> spp.	<b>268</b>	<b>279</b>	<b>300</b>
Total	<b>262</b>	<b>282</b>	<b>309</b>

The estimates are based on six-parameter Weibull models (W6p). Values of significant models are marked in bold type. n.a. = not available.

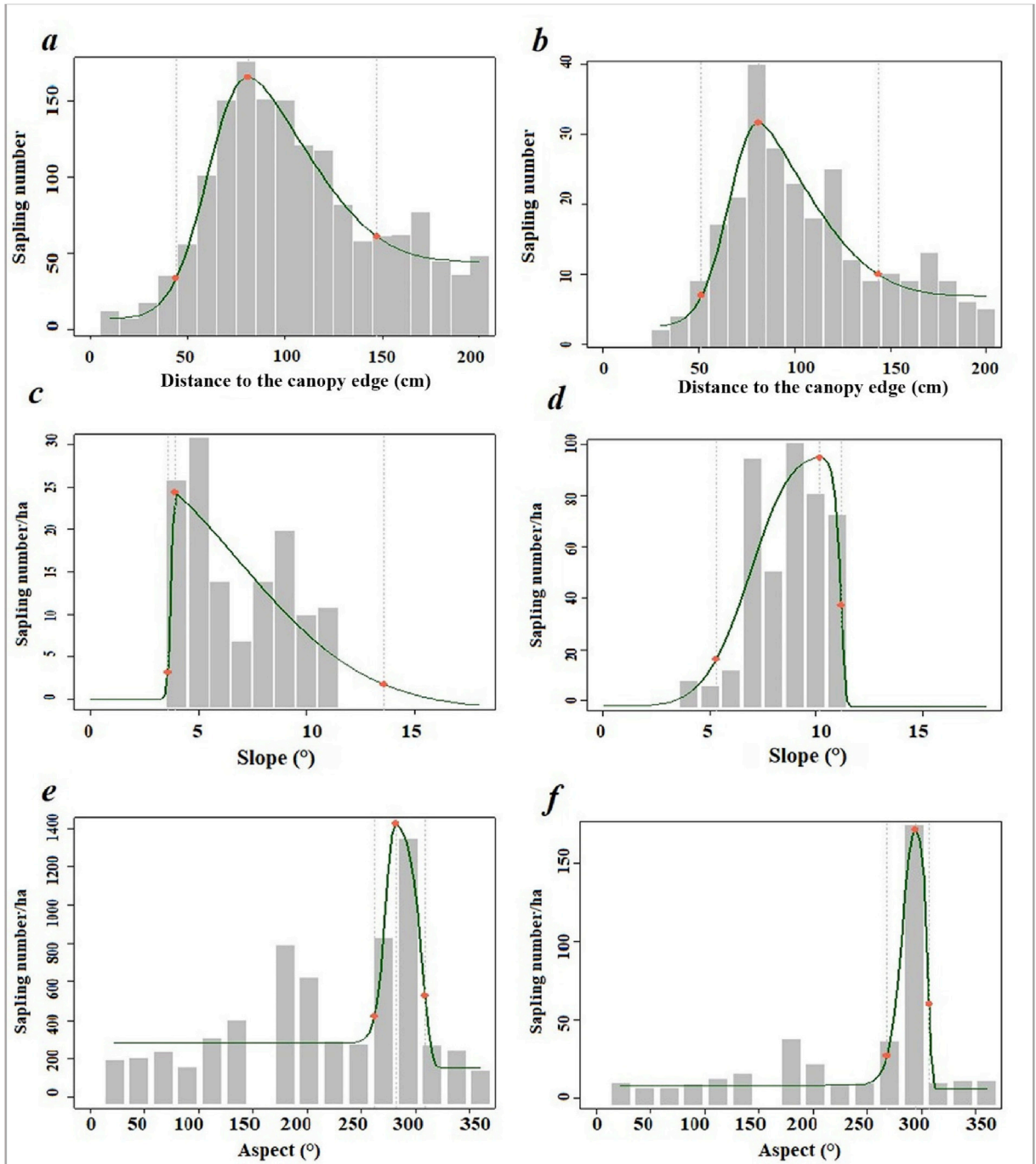
of the W6p models of sapling distribution for distance from the edge, 55% of the models of sapling distribution with respect to slope and, 78% in relation with geographical aspect provided good enough fits to describe the observed distribution (Table 4).

## 4. Discussion

### 4.1. Spatial structure of the regeneration

The initial hypothesis that natural regenerated saplings almost always occur in clusters in canopy gaps was not confirmed. Indeed, regeneration was marginal inside canopy gaps larger than 16 m<sup>2</sup>, and the sapling density was ten times higher in the tree canopy cover than in the gaps (Table S1), bordering the canopy cover. On average, the first maximum number of saplings was detected at about 81 cm from the gap edge, inside the tree canopy cover and under trees growing at the gap edges (Table 3, Fig. 4). These findings contrast directly with the gap dynamics described in many previous studies (e.g. Yamamoto, 2000; Pham et al., 2004; Schliemann and Bockheim, 2011). In uneven aged pine-oak forests, gap dynamics have been reported to lead to clusters of naturally regenerated trees inside the gaps (Rodríguez, 1958; Wehenkel et al., 2011).

Gap dynamics suggest that when small openings (gaps) are formed in a forest canopy, advanced regeneration (established before gap formation) within gaps is sustained and/or new seedlings become established in the gaps. Seedlings of shade-intolerant species can colonize larger gaps, frequently with uncovered mineral soils, while in smaller gaps, advanced regeneration of shade-tolerant species predominates (van der Maarel, 1988; Yamamoto, 2000; Muscolo et al., 2014). In a study of a species-rich temperate deciduous forest in the USA, Busing (1994) found that regeneration of most species tended to be greater in the gaps, and that almost 100% regeneration of shade-intolerant species occurred in gaps. On the other hand, Ward and Parker (1989) did not observe any differences in regeneration density under a closed canopy and inside the gaps in an old-growth forest in east-central Indiana, USA. However, the horizontal spatial distributions of the studied tree species were amazingly similar (Table 3 and Table S1, Fig. 4), i.e., the hypothesis of species-specific differences was not confirmed. Even if the studied species had different seed dispersal, there must have been a force which has formed these ring-type spatial patterns around the gaps and set a boundary, regardless of the species' behaviours and shade tolerance degree.



**Fig. 4.** Histograms of number of saplings in relation to distance (cm) from the edge of the nearest canopy gap to the tree stem bases (below tree crowns) and of sapling number per hectare in relation to slope and geographical aspect ( $0\text{--}359^\circ$ ), including the fitted six-parameter Weibull model (W6p) curves; cardinal sapling numbers (orange dots) were identified from the fitted W6p, corresponding to the beginning of the curve slope/rise (outbreak), curve maximum (peak) and end of the curve slope/decrease (collapse): a) number of saplings among all studied tree species vs. distance (in cm) to the edge of the nearest canopy gap, b) number of *Pinus durangensis* saplings vs. distance (in cm) from the edge of the nearest canopy gap, c) number of *Arbutus* spp. saplings  $\text{ha}^{-1}$  vs. slope, d) number of *Quercus* spp. saplings  $\text{ha}^{-1}$  vs. slope, e) number of saplings  $\text{ha}^{-1}$  among all studied tree species vs. geographical aspect (in degrees), f) number of *Pinus leiophylla* saplings  $\text{ha}^{-1}$  vs. geographical aspect (in degrees). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

**Table 4**

Six-parametric ( $p_1$ - $p_6$ ) Weibull (distribution) models of number of saplings or number of saplings within a maximum distance of 2 m from the gap edge in the canopy covered area, with respect to the distance from the edge of the canopy cover (calculated for mean sapling number), slope and geographical aspect (calculated for mean number of saplings ha<sup>-1</sup>).

Tree species	Arb	Jd	Pa	Pd	Pe	Pl	Ps	Qu	Total
<b>n in total</b>	66	<b>510</b>	<b>150</b>	<b>242</b>	<b>286</b>	51	<b>10</b>	<b>167</b>	<b>1,482</b>
<b>Distance (cm)</b>									
$p_1$	0.855	<b>0.920</b>	<b>0.909</b>	<b>0.945</b>	<b>0.930</b>	0.881	<b>0.749</b>	<b>0.952</b>	<b>0.964</b>
$p_2$	60.17	<b>65.16</b>	<b>55.04</b>	<b>69.36</b>	<b>63.37</b>	59.12	<b>105.57</b>	<b>75.17</b>	<b>65.31</b>
$p_3$	99.98	<b>12.24</b>	<b>8.96</b>	<b>7.09</b>	<b>3.06</b>	29.81	<b>100.03</b>	<b>8.34</b>	<b>5.049</b>
$p_4$	-0.112	<b>0.158</b>	<b>0.251</b>	<b>0.175</b>	<b>0.287</b>	0.409	<b>0.332</b>	<b>0.281</b>	<b>0.260</b>
$p_5$	200.03	<b>137.13</b>	<b>106.11</b>	<b>108.01</b>	<b>104.23</b>	81.26	<b>113.07</b>	<b>111.19</b>	<b>115.9</b>
$p_6$	2.459	<b>3.508</b>	<b>2.400</b>	<b>3.270</b>	<b>5.417</b>	5.306	<b>32.832</b>	<b>5.316</b>	<b>3.543</b>
$r^2$	0.542	<b>0.946</b>	<b>0.769</b>	<b>0.866</b>	<b>0.876</b>	0.541	<b>0.999</b>	<b>0.872</b>	<b>0.968</b>
<b>p value</b>	0.001	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.001	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>AIC</b>	11.0	<b>-28.0</b>	<b>-2.6</b>	<b>-17.6</b>	<b>-17.8</b>	14.6	<b>-93.9</b>	<b>-10.9</b>	<b>-43.9</b>
<b>BIC</b>	1.4	<b>-37.0</b>	<b>-11.6</b>	<b>-26.9</b>	<b>-26.9</b>	5.3	<b>-105.7</b>	<b>-20.4</b>	<b>-52.9</b>
<b>Slope (°)</b>									
$p_1$	<b>1.000</b>	0.724	0.824	1.388	<b>0.355</b>	<b>0.037</b>	<b>41.382</b>	<b>1.02</b>	0.734
$p_2$	<b>3.77</b>	52.37	15.83	56.11	<b>35.57</b>	<b>67.06</b>	<b>12.18</b>	<b>7.31</b>	15.69
$p_3$	<b>44.98</b>	9.93	100.12	47.34	<b>10.18</b>	<b>9.94</b>	<b>-67.09</b>	<b>4.96</b>	100.00
$p_4$	<b>-0.035</b>	0.078	-0.005	-1.281	<b>0.000</b>	<b>0.039</b>	<b>-1.003</b>	<b>-0.022</b>	0.104
$p_5$	<b>9.12</b>	5.18	16.55	148.63	<b>4.81</b>	<b>0.68</b>	<b>18.66</b>	<b>11.21</b>	11.74
$p_6$	<b>2.15</b>	9.11	53.89	49.16	<b>4.79</b>	<b>6.27</b>	<b>106.87</b>	<b>61.26</b>	100.00
$r^2$	<b>0.800</b>	0.290	0.293	0.000	<b>0.715</b>	<b>0.827</b>	<b>0.818</b>	<b>0.860</b>	0.281
<b>p value</b>	<b>0.000</b>	0.017	0.016	1.000	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	0.019
<b>AIC</b>	<b>-3.5</b>	7.9	18.0	8.6	<b>2.9</b>	<b>-16.4</b>	<b>-14.1</b>	<b>-5.5</b>	8.3
<b>BIC</b>	<b>-12.7</b>	-1.3	8.9	2.5	<b>-6.3</b>	<b>-25.5</b>	<b>-23.3</b>	<b>-14.7</b>	-0.8
<b>Geographical aspect (°)</b>									
$p_1$	<b>0.945</b>	0.833	0.781	<b>0.851</b>	<b>0.775</b>	<b>0.953</b>	<b>0.882</b>	<b>0.900</b>	<b>0.807</b>
$p_2$	<b>256.03</b>	310.43	175.35	<b>286.51</b>	<b>268.76</b>	<b>283.01</b>	<b>287.56</b>	<b>272.84</b>	<b>272.92</b>
$p_3$	<b>39.97</b>	2.26	100.00	<b>45.36</b>	<b>77.46</b>	<b>40.19</b>	<b>100.00</b>	<b>100.00</b>	<b>52.06</b>
$p_4$	<b>0.0481</b>	0.259	0.193	<b>0.076</b>	<b>0.161</b>	<b>0.032</b>	<b>0.002</b>	<b>0.073</b>	<b>0.117</b>
$p_5$	<b>300.18</b>	313.86	229.09	<b>311.61</b>	<b>297.63</b>	<b>306.69</b>	<b>308.38</b>	<b>300.48</b>	<b>307.30</b>
$p_6$	<b>25.30</b>	100.00	3.56	<b>84.17</b>	<b>10.00</b>	<b>10.00</b>	<b>100.00</b>	<b>95.77</b>	<b>42.35</b>
$r^2$	<b>0.977</b>	0.461	0.487	<b>0.770</b>	<b>0.690</b>	<b>0.964</b>	<b>0.588</b>	<b>0.860</b>	<b>0.726</b>
<b>p value</b>	<b>0.000</b>	0.003	0.002	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>	<b>0.000</b>
<b>AIC</b>	<b>-40.0</b>	14.8	12.1	<b>-6.3</b>	<b>5.7</b>	<b>-36.3</b>	<b>9.8</b>	<b>-13.4</b>	<b>-1.6</b>
<b>BIC</b>	<b>-49.7</b>	5.1	2.4	<b>-16.0</b>	<b>-4.0</b>	<b>-46.0</b>	<b>0.1</b>	<b>-23.1</b>	<b>-11.2</b>

Note:  $p_1$  to  $p_6$  = estimated model parameters,  $n$  = individual number,  $r^2$  = Pearson coefficient of determination,  $p$  value = probability value, AIC = Akaike information criterion, BIC = Bayesian information criterion, n.a. = not available; significant models after Bonferroni correction are marked in bold type. Arb: *Arbutus* spp., Jd: *Juniperus depepeana*, Pa: *Pinus arizonica*, Pd: *Pinus durangensis*, Pe: *Pinus engelmannii*, Pl: *Pinus leiophylla*, Ps: *Pinus strobiformis*, Qu: *Quercus* spp.

The climatic conditions of the study region are characterized by monsoon with a pronounced dry season (Fig. S1; Douglas et al., 1993; Liebmann et al., 2008). This may greatly limit the amount of water available for seedling establishment and cause high evaporative stress in the dry season (McLaren and McDonald, 2003).

Extreme weather events or periods can impact terrestrial biota and also forest regeneration (Parmesan et al., 2000). The drought that occurred in 2011 in the Sierra Madre Occidental was reported to be the worst experienced in the last 70 years (Reuters/EP, 2011). However, the drought in 2012 was even more severe in the study region (Fig. S1). By 2011 and 2012, many of the studied saplings were still seedlings, and therefore probably susceptible to extreme cavitation (Domec et al., 2004), as also confirmed by the smaller number of saplings and increase in the absolute and relative frequency of the drought stress tolerant species *Juniperus depepeana* (Sáenz-Romero et al., 2014) in the first diameter class (Fig. 2b and Fig. S3). Seedlings and saplings (especially those growing in gaps) may have died during these extreme droughts, thus partly explaining why regeneration in the study area was more abundant under the canopy cover. Indeed, the saplings grew together with the upperstorey trees in our study, as revealed by the bivariate  $K$ -function analysis (Fig. 3b). However, a distance similar to the modelled mean distance of 77 cm was maintained between the tree stems at the edge of the gap, probably caused by competition for growing space and soil moisture (Nambiar and Sands, 1993; Morrissey et al., 2008).

We attribute these findings to the nurse effect of trees, which ameliorate the abiotic effects (particularly the extreme weather events, such as the drought and solar radiation in 2011 and 2012 in the study region) on seedlings and saplings and facilitate their establishment under canopies (Callaway and Walker, 1997). Commonly documented ameliorative influences of the nurse plant canopy include cooler temperatures and lower evaporative stress, increased soil moisture, protection against herbivores and greater availability of nutrients (Callaway and Pugnaire, 1999). Although light in the understory is an important factor for regeneration, and is often a limiting factor particularly in dense forests, in the relatively open forests of the studied area probably it is not the most important factor. Whereas in closed canopies only a very small fraction (<5%) of the solar radiation above the canopy reach the understory (Chazdon, 1988; Chazdon and Pearcy, 1991), in more open, xeric

forests full sunlight enters through the larger openings (sun patches) (Smith et al., 1989; Smith and Berry, 2013). Moreover, light indirectly affects soil temperature and moisture by decreased solar heating (Bieleski, 1959). Carbajal-Navarro et al. (2019) showed that the average daily air temperature and its variations were lower below nurse plants than in open areas. The lower temperatures could result in a lower vapor pressure deficit, reducing transpiration.

Nurse-plant effects have been tested and used in effective reforestation and restoration strategies in different ecosystems (Gómez-Aparicio et al., 2004; Walker and Powell, 1999; Aerts et al., 2007; Zhao et al., 2007; Yoshihara et al., 2010). For example, positive effects of *Lupinus elegans* as a nurse plant have been observed in seedlings of *Pinus montezumae*, *P. pseudostrobus* and *Abies religiosa* in a Mexican temperate forest (Blanco-García et al., 2011). Muhamed (2019) found that seedlings and saplings of *Pinus brutia* were distributed in an aggregation pattern in comparison to the randomized pattern of the parent trees, and positively correlated with the presence of shrubs, particularly with *Quercus* shrubs. As found by Molina-Montenegro et al. (2016) for a semiarid community in Chile, in the pine-oak forests from the Sierra Madre Occidental, the nurse tree effect may therefore represent a key mechanism for increasing the establishing of native tree species.

The nurse-effect is also important as protection against grazing. Although the effect of cattle grazing was not analyzed in relation to forest regeneration in this study, some reports indicate that several pine and oak species are very sensitive to cattle grazing (Quintana-Ascencio et al., 1992; Reyna et al., 2019) and that tree saplings are more protected when surrounded by taller vegetation, as observed by Vandenberghe et al. (2007) for wooded mountain pastures in Switzerland.

Establishment of complementary plantations has been also reported as a method of improving forest regeneration. Regeneration methods such as the irregular group shelterwood method (Expanding Gap Silviculture "Femelschlag") have been considered as a way of enhancing the restoration of forests affected by disturbances (Raymond et al., 2009).

#### 4.2. Influence of slope, geographical aspect and soil properties on the spatial distribution of natural regeneration

Our hypothesis of aspect-dependent forest regeneration was confirmed. Saplings were more abundant at gap edges located on the northwest facing slopes (Table 3, Fig. 4), which are shaded for longer periods than the southern facing slopes (Brooks and Merenlender, 2001). It is not clear why regeneration was limited on the eastern and northeastern facing slopes; however, it was possibly due to the fact that clouds and precipitation occur most frequently in the afternoon during the monsoon season in the Sierra Madre Occidental (Rowe et al., 2008). In addition, a large amount of the humidity in the study area comes from the Pacific Ocean, i.e. from the west. During cloudy or rainy afternoons, solar radiation, which usually impacts vegetation on western slopes in the northern hemisphere, cannot exert its full drying effect. This additional shading and cooling effect is much weaker in the mornings, when the solar radiation strikes the eastern facing slopes.

The assumption that natural forest regeneration is more abundant in gently sloping areas was not confirmed. This may be because the more abundant leaf litter remaining on the ground in these relatively flat areas, has an adverse influence on forest regeneration (Koroleff, 1954; Bueno and Baruch, 2011). Moreover, different tree species seem to prefer different types of slopes (Table 3) probably because of their different seed dispersal and regeneration strategies. Ustin et al. (1984) suggested that aggregations of seedlings were the result of differential germination and seedling survival, which may be susceptible to water and thermal stresses during prolonged sunfleck exposures. As for the trees in our area, *Arbutus* (the madrone, a relative of the strawberry tree) produces fleshy fruits and disperses its seeds via ingestion by vertebrate animals (mostly birds and mammals, endozoochory). *Quercus* and *Juniperus* mainly disperse their seeds by seed-caching granivorous birds and/or mammals (synzoochory), which store the seeds in small cavities in the ground or tree trunks. The seeds of *Pinus* are typically dispersed by wind (anemochory) (Gottfried, 1992; Cortés-Flores et al., 2013), except for stone pines, such as *Pinus strobiformis*, in which seed dispersal is often mediated by seed-caching animals (e.g. corvids and tree squirrels) (Siepielski and Benkman, 2007). These different strategies could lead to differences in the spatial distribution of the saplings.

## 5. Conclusions

The study findings have important implications for the Mexican continuous-cover forest management system in the northern zone of the Sierra Madre Occidental, the region with the most extreme, continental climate in this mountain range. Assuming a random spatial sapling distribution, the mean sapling density of 393 individuals per ha could be sufficient to ensure the regeneration of harvested stands supported by mostly balanced reversed J shaped diameter distributions of the studied tree species (Figs. S2 and S3; Wehenkel et al., 2011). Moreover, a considerable shift in species composition from upperstory trees to saplings was not detected (Table S1). However, the largely lack of saplings in larger canopy gaps could result in fragmented forest stands. Contrary to previous reports of higher regeneration in the gaps, in comparison with the canopy cover, in uneven aged pine-oak forests, we found that the first maximum density of saplings fashioned ring-type spatial patterns around the gaps, below the crowns of nurse-trees growing at the edges between the canopy cover and the gaps.

We recommend adapting or changing the current forest management system to improve continuous forest regeneration including adaptive silviculture. Management should place greater focus on the nurse effects of the remaining vegetation, as an efficient tool for enhancing regeneration. Canopy gaps created by logging should be kept as small as possible and such gaps should be avoided on steep south and south-east facing slopes, especially if forest regeneration is not sufficient or secure below the trees remaining after harvesting.



We also strongly support i) research on the effects of cattle grazing on natural regeneration in the region and ii) reduction of livestock pressure, which is essential to support forest renewal. Complementary reforestation, in addition to maintenance of the few saplings growing within the gaps, may help enhance forest regeneration. Finally, the use of alternative regeneration methods, such as an irregular group shelterwood method (Expanding Gap Silviculture "Femelschlag"), should also be considered, in order to promote natural regeneration more purposefully.

### Declaration of competing interest

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

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01074>.

### Author contributions

CW conceived and designed the experiments; JFMN & JHV conducted sampling, JFMN and CW analyzed the data and prepared figures and tables; JFMN & CW contributed reagents/materials/analysis tools; all authors discussed the results; CW and JFMN wrote the paper; MSGE, JCHD, CALS, PA, CEBS & JFMN contributed to the writing of drafts of the paper and to the final edition.

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