



# Spatial patterns of Mexican beech seedlings (*Fagus grandifolia* subsp. *mexicana* (Martínez) A.E. Murray): influence of canopy openness and conspecific trees on recruitment mechanisms

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## Abstract

• **Key message** Recruitment strategies of Mexican beech seedlings depend on mother tree distribution and light incidence in early stages of development. Spatial patterns are also affected by the structure and composition of tree species within Mexican beech forests.

• **Context** Canopy openness and conspecific trees play a key role in Mexican beech spatial distribution and might strongly influence ecosystem functioning in the Tropical Montane Cloud Forest. The observed relationship between diameter at breast height of conspecific trees and the spatial distribution of beech seedlings indicates that structure and composition of tree species are crucial for the establishment and survival of seedlings, providing protection during the first developmental stages.

• **Aims** To describe the spatial patterns of beech seedlings' distribution after a masting event and to evaluate the association of these patterns with canopy openness, conspecific tree distribution, and occurrence of other canopy species.

• **Methods** We sampled individual Mexican beech seedlings on two highly conserved beech forests. We selected 100 subplots (10 × 10 m) on each one to measure seedlings and spatial attributes. We counted the number of beech seedlings and number of mature trees species on each subplot. In addition, we measured the levels of canopy openness and the diameter at breast height for all mature trees in each subplot. Spatial pattern of beech seedlings and their association with adult trees and other species were examined.

• **Results** Mexican beech seedlings showed significant pattern of spatial aggregation. Significant associations were found between beech seedlings, canopy openness, and beech tree adults, while significant disassociations exist among beech seedlings and other species of trees such as *Quercus meavei*, *Q. delgadoana*, *Q. trinitatis*, and *Magnolia schiedeana*.

• **Conclusion** The presence of oak species and *Magnolia schiedeana* in the surroundings and the structure and composition within forests may play a key role in the maintenance of the specific micro-environmental conditions required by Mexican beech recruitment after a masting event.

**Keywords** Beechnuts · *Fagus grandifolia* subsp. *mexicana* · Masting year · Recruitment · Seedlings · Spatial aggregation

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## 1 Introduction

Spatial patterns during seedlings' recruitment are an important factor influencing the dynamics of forest communities (Kunstler et al. 2004; Nathan and Muller-Landau 2000). Forest regeneration is the result of sexual and asexual reproduction, seed dispersal, and recruitment such as seed germination and seedling survival, which are a crucial stage in the regeneration of beech forests (Beaudet and Messier 2008; Kunstler et al. 2004; E Silva et al. 2012). Seed dispersal is strongly dependent on the spatial disposition of mature trees, which protect seedlings from direct sunlight during the first developmental stages and causes one-sided competition for light (Alvarez-Aquino and Williams-Linera 2002; Camacho-Cruz et al. 2000; Queenborough et al. 2007; Wang et al. 2012). The sheltering effect, mostly associated with micro-environmental factors (i.e., canopy openness, pH, moisture, leaf litter), probably has a main effect on the structure and floristic composition of forests ecosystems (Leibold and McPeck 2006; Messaoud and Houle 2006; Peña et al. 2011; Tuomisto et al. 2012). Specifically, the type of spatial distribution shown by seedlings and adult trees (i.e., regular, aggregated or random) has been used to determine the dispersal capabilities and recruitment probabilities of plants (Camarero et al. 2005; Dusan et al. 2007; Meier et al. 2010; Snell et al. 2014; Szymura et al. 2015).

In septentrional beeches, root suckers play a key role increasing competitiveness and survival under adverse conditions (Beaudet and Messier 2008). Peters (1992) registered asexual reproduction by multi-stemmed plants in northern beech individuals. Asexual reproduction is more important and common than sexual reproduction in northern counterparts. The regeneration ecology of Mexican beech is different to northern species from the same genus, because the vegetation type where it grows in Mexico, the Tropical Montane Cloud Forest, is a favorable environment for shade-tolerant tree species.

In this study, we analyzed the spatial patterns of Mexican beech seedlings (*Fagus grandifolia* subsp. *mexicana* (Martínez) A.E. Murray), a Miocene relict species endemic to the Tropical Montane Cloud Forest in eastern Mexico. This forest community covers approximately 144.54 ha through a series of fragmented patches at altitudes of 1400–2000 m in the states of Hidalgo, Nuevo León, Puebla, Tamaulipas, and Veracruz (Montiel-Oscara et al. 2013; Peters 1992; Rodríguez-Ramírez et al. 2013; Rowden et al. 2004). Mexican beech is considered an endangered species under Mexican law (González-Espinosa et al. 2011; SEMARNAT 2010) and is currently threatened by human activities, such as illegal logging and deforestation (Téllez-Valdés et al. 2006; Williams-Linera et al. 2003).

The beechnuts of Mexican beech are shade-tolerant and can survive under low light incidence (Godínez-Ibarra et al.

2007). These beechnuts fall from the mature trees mainly on August, the more humid month of the year. They quickly respond to humidity when they fall to the ground. Seemingly, these beechnuts of this species have low dormancy (approximately 1 month sensu Peters (1992)) and personal observations; however, they respond to canopy openness by accelerating their development (Gazol and Ibáñez 2010; Pedraza-Pérez and Williams-Linera 2005). Development and growth of seedlings may also be affected by canopy openness, inter-specific competition (or cooperation sensu Kiers et al. (2011)), and accumulation of leaf litter (Collet and Chenost 2006; Jennings et al. 1999). Moreover, Mexican beech is characterized by the occurrence of synchronous, inter-annual variation in reproductive effort, commonly known as “masting events” at 2- to 8-year intervals (Ehnis 1981; Godínez-Ibarra et al. 2007; Pérez-Rodríguez 1999; Rodríguez-Ramírez et al. 2013). Unfortunately, the adaptive significance and evolutionary precursors of masting events have not yet been fully determined (Kelly 1994; Kelly and Sork 2002). The resource-matching hypothesis provides the most parsimonious explanation for masting (Monks and Kelly 2006; Sork et al. 1993). This hypothesis states that plants allocate a constant fraction of assimilated carbon for reproduction each year. Thus, highly favorable climatic conditions in specific years promote high rates of carbon assimilation and thus a greater beechnut production (Piovensan and Adams 2001, 2005).

In this context, the structure and floristic composition of forest ecosystems are intimately related to micro-environmental factors such as proportion of mature healthy trees, canopy openness, soil type, pH, and moisture (Taugourdeau and Sabatier 2010; Peña et al. 2011; Rodríguez-Ramírez et al. 2016). The spatial distribution of seedlings is strongly correlated by the random opening and closure of the canopy, which produces micro-habitat heterogeneity (Meier et al. 2010; Offord et al. 2014; Barna and Bosela 2015). Thus, the study of the spatial pattern of seedlings can aid in the understanding of the biotic and abiotic requirements for the establishment and survival of currently endangered forest species, such as Mexican beech (Godínez-Ibarra et al. 2007; Övergaard et al. 2007; Hardiman et al. 2011).

Mexican beechnuts are dispersed randomly near the mother trees in a segregate pattern (Peters 1995, 1997). After the masting event, germination is extensive and the produced seedlings compete for light and water (Godínez-Ibarra et al. 2007). Moreover, canopy openness is an essential factor for beech seedling development, notwithstanding the shade-tolerant natural of beech (E Silva et al. 2012). The ecology of beech seedlings has been extensively studied in northern beeches, but few studies focusing on the spatial distribution at local level have been done (i.e., Gazol and Ibáñez (2010), Godínez-Ibarra et al. (2007), Kunstler et al. (2004) and Shibata et al. (2002)).

In this study, we describe for the first time the spatial patterns of Mexican beech seedlings within a beech-dominated Tropical Montane Cloud Forest in the state of Hidalgo, Mexico. Our aims were (1) to describe the spatial patterns of beech seedlings distribution after a masting event and (2) to evaluate the association of these patterns with canopy openness, conspecific tree distribution, and occurrence of other canopy species. With this context, the present analysis provides a deeper understanding of the auto-ecological processes that affect the establishment and survival of Mexican beech in the Tropical Montane Cloud Forest.

## 2 Materials and methods

### 2.1 Study sites

The study sites are located within two extensive and highly preserved forest stands of Mexican beech in the state of Hidalgo: La Mojonera, Zacualtupán de Ángeles (20° 38' N, 98° 36' W; 1780–1950 m a.s.l.), and Medio Monte, San Bartolo Tutotepec (20° 24' N, 98° 14' W; 1800–1944 m a.s.l.; Fig. 1(A), Table 1; Rodríguez-Ramírez et al. 2013). These sites have a temperate Cb climate (sensu García (1988)) characterized by mild temperatures, dry cool season from November to January, dry warm season from early February to May, cool summer (June to July), and wet cool season from August to October (Peters 1995; Williams-Linera 2007). The high frequency of fog and precipitation causes persistent moisture (60–85%) throughout the year (García 1988; Tinoco-Rueda 2009). The dominant lithologies are vitric (Tv) and humic (Th) andosols (FAO-UNESCO; Batjes 1997) with a slimy sandy-clay loam texture and acidic pH values ranging between 4 and 6 (Peters 1995, 1997).

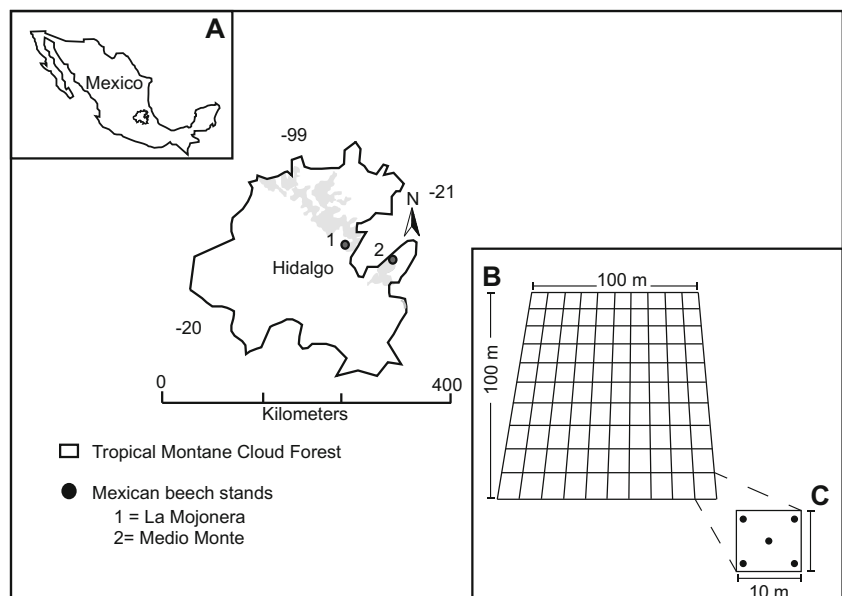
La Mojonera has one of the most extensive Mexican beech forests in Mexico (42.5 ha); it is the most studied and shows the least disturbance by human activities (Rowden et al. 2004; Rodríguez-Ramírez et al. 2013). In addition to Mexican beech (*Fagus grandifolia* subsp. *mexicana*), the high-canopy (> 20 m) of the forest is composed of *Pinus patula* Schltld. & Cham., *Quercus trinitatis* Trel., *Liquidambar styraciflua* L., and *Magnolia schiedeana* Schltld. The mid-canopy (10–20 m) of the forest is dominated by *Clethra mexicana* DC., *Befaria aestuans* L., and *Quercus delgadoana* S. Valencia, Nixon & L. M. Kelly.

The Mexican beech forest at Medio Monte (34.25 ha) is located on slightly rugged terrains and is characterized by trees reaching up to 25 m in height. The forest is dominated by *F. grandifolia* subsp. *mexicana*, *Magnolia schiedeana*, and *Quercus meavei* Valencia-A., Sabás & Soto. The mid-canopy of the forest is mainly composed of *Clethra mexicana*, *Q. delgadoana*, and *Q. trinitatis*, whereas the low canopy consists mainly of *Cyathea fulva* (M. Martens & Galeotti) Fée and *Dicksonia sellowiana* Hook. (Table S1). A more detailed description of plant species composition and structure in the studied forests can be found in Rodríguez-Ramírez et al. (2016).

### 2.2 Sampling protocol

Individual beech seedlings were counted (December 2012 to January 2013) shortly after the occurrence of a masting event (August–September 2012). A permanent plot of 100 × 100 m<sup>2</sup> was set up in representative areas of forest stands, as far as possible from human settlements and roads. In each permanent plot, we defined 100 subplots of 10 × 10 m (Fig. 1(B); Roberts-Pichette and Gillespie 1999). We used a manual counter (Base Mount Tally Counter) in each subplot to

**Fig. 1** (A) Geographical location of the two study sites of *Fagus grandifolia* subsp. *mexicana* (Martínez) A.E. Murray (Mexican beech) in the Tropical Montane Cloud Forests of the Sierra Madre Oriental, Mexico. (B) Schematic representation of the 100 × 100 m plots subdivided into 10 × 10 m subplots



**Table 1** Geographic characteristics at the two sites of *Fagus grandifolia* subsp. *mexicana* (Martínez) A.E. Murray in the mountains of the Sierra Madre Oriental of eastern Mexico

		LA MOJONERA	MEDIO MONTE
Area (ha)		42.5	34.25
Latitude (N)		20° 38' 33"	20° 24' 50"
Longitude (W)		98° 36' 51.8"	98° 14' 24"
Elevation (m a.s.l.)		1780–1950	1800–1944
Slope (degrees)	Max	37.8	21.5
	Min	1.8	0.45
Diameter at breast height (cm)	Max	118	110
	Min	54	43
Height (m)	Max	25	28
	Min	14	15

quantify each beech seedling with a height  $\leq 10$  cm (Peters 1995). In each subplot, all mature trees were measured following Kindt and Coe (2005) method; these authors considered that individual trees reach maturity when they achieve (1) a diameter at breast height  $\geq 15$  cm, and (2)  $\geq 30$  m high. All the trees were identified to the species level and compared with herbaria specimens from HGOM (Universidad Autónoma del Estado de Hidalgo) and the Herbario del Instituto de Ecología, A.C., México (IE-XAL).

In order to evaluate the influence of canopy openness on the distribution of Mexican beech seedlings, we measured canopy openness for each subplot using a canopy densitometer (Model A, Lemmon 1956; Fiala et al. 2006) between 9:00 am and 12:00 pm to standardize the daily sunlight fluctuation. In each subplot, we performed five independent measurements of canopy openness in four different orientations (i.e., north, south, east, and west; Fig. 1(C)). The data obtained through the measurements were averaged for statistical analyses.

### 2.3 Spatial analyses of beech seedlings, canopy openness, and conspecific trees

We described the spatial pattern of beech seedling distribution and evaluated its association with the diameter at breast height of mature trees of different species and canopy openness using the software SADIE (Spatial Analysis by Distance IndicEs; Perry 1998; Perry and Dixon 2002; Perry et al. 2006). SADIE incorporates spatial information of the counted data from geographically referenced points (Perry et al. 1999), allowing to identify the exact location of seedling hotspots.

This method is based on “distance regularity” ( $D$ ), which measures the total distance involved in passing from the observed spatial arrangement of counts to move to a regular arrangement where all units have the same value of the variable under study. To calculate  $D$ , which is characterized by a high proportion of zeros and a non-normal distribution,

SADIE uses the transportation algorithm from the linear programming literature. One main advantage of this method is that the input data does not need to present a normal distribution, show isotropism (i.e., no environmental changes), or be regularly spaced (Maestre and Cortina 2002; Maestre et al. 2003). Thus, analyses using SADIE are not limited by these restrictions and the results are conditioned on the levels of heterogeneity present in the data (Bell 1998; Perry et al. 1996; Perry et al. 1999).

SADIE evaluates the magnitude and significance of  $D$  (distance to regularity) by comparing the observed  $D$  value with those obtained from randomized datasets. In the present case, the observed distribution of beech seedlings across subplots was compared to 1000 randomly generated distributions (i.e., random number of seedlings per subplot). SADIE provides two complementary measures of the spatial structure of count data. First, the index of aggregation,  $I_a$ , is a global measure of the degree of aggregation or a variable, which was calculated for each data set to determine overall 23,433 randomizations each, where  $I_a = 1$  indicates random arrangement of counts of no significant spatial pattern;  $I_a > 1$ , aggregated arrangement giving clusters of observed counts; and  $I_a < 1$ , regular arrangement of counts (Perry and Dixon 2002). The probability  $P_a$  tests for deviations from random dispersal where  $P_a > 0.975$  indicates regular dispersal;  $P_a < 0.025$ , spatial aggregation; and  $0.025 < P_a < 0.975$ , randomness (Perry 1998; Perry and Dixon 2002). Second, the clustering indices ( $v$ ) are a parameter calculated for each point in the data base which were estimated for subplots with Mexican beech seedling densities above ( $v_i > 1.5$ ) and below the plot's average ( $v_j < -1.5$ ) (Perry et al. 1999; Winder et al. 2001; Maestre and Cortina 2002; Perry and Dixon 2002) where subscripts  $i$  and  $j$  indicate patches and gaps, respectively. Mean clustering indices ( $\overline{v_i}$  and  $\overline{v_j}$ ) were also calculated for each data set and compared with their corresponding values from the 23,433 randomizations to test the overall clustering at 5% level.

## 2.4 Evaluating spatial association

The local spatial association was measured using an index  $X_k$  based on similarities between clustering indices of the variables (i.e., beech seedling vs. canopy openness). Positive values of  $X_k$  ( $> 0$  indicates a positive spatial association) were indicated by a coincidence of two patches or two gaps while negative association (values  $< 0$  indicate a lack of concordance between variables) resulted from a patch coinciding with a gap in both subplots (Perry 1998). We estimated a general  $X$  index from the mean values for each subplot in the two study sites, which summarizes the spatial pattern of beech seedling distribution in relation to mature trees and canopy openness (sensu Winder et al. (2001), Perry and Dixon (2002), and Perry et al. (1999)). The significance of the general  $X$  index was evaluated through 1,000 randomizations of clustering indices ( $v$ ) (Dutilleul 1993) for seedlings, adult trees, and light incidence. For this comparison,  $P$  values  $< 0.025$  indicated a significant spatial association, whereas  $P$  values  $> 0.975$  were indicative of a significant spatial disassociation.

Finally, we visualized the observed patterns of spatial aggregation and association for beech seedlings across the two study sites using Surfer® v. 14 (Golden Software Inc., CO, USA) with the red-blue method (Perry et al. 1996; Perry and Dixon 2002).

## 3 Results

### 3.1 Spatial patterns of Mexican beech seedlings

Contour maps of the index of clustering visually indicate the spatial distribution of the main patches and gaps within the sampled plots. In the two studied sites, Mexican beech seedlings showed significant pattern of spatial aggregation (Fig. 2(1A)—La Mojonera:  $I_a > 2$ ,  $P_a$  0.0002; Fig. 2(2A)—Medio Monte:  $I_a > 1$ ,  $P_a$  0.063; Table 2). Overall, we also observed significant spatial association in the distribution of *Fagus*' seedlings ( $I_a > 1$ ;  $P_a$  0.0002) and canopy openness ( $I_a > 1$ ;  $P_a < 0.0184$ ; Fig. 2).

### 3.2 Association of Mexican beech seedlings

The spatial distribution of beech seedlings showed a significant association with below-canopy light incidence, with a value  $\geq 80\%$  but lower than 100% ( $P < 0.025$ ; Fig. 2(1), (2A+B)). We found significant associations between the spatial distribution of beech seedlings and the average diameter at breast height of conspecific trees in the two Mexican beech stands (Fig. 2(1A+B) and (2A+B); Table 2). However, we observed a negative correlation between the number of beech seedlings per subplot and the

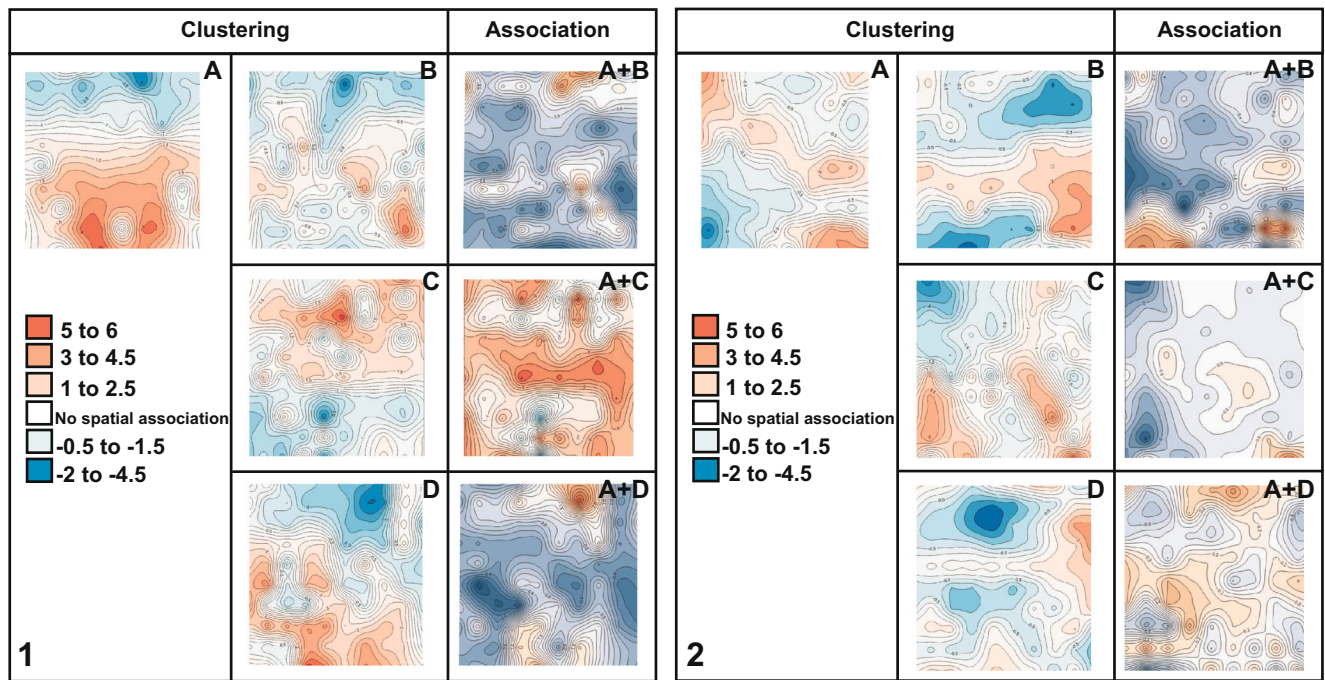
diameter at breast height of mature beeches in La Mojonera:  $r = -0.08$ ,  $P = 0.05$ ; Fig. 2(1A+C). However, there was no evidence of a spatial association between beech seedlings and adult beeches in Medio Monte ( $X_k = 0.016$ ;  $P = 0.446$ ; Fig. 2(2A+C)). We also found a spatial disassociation between the distribution of beech seedlings and the occurrence of canopy tree species other than *Fagus*. More specifically, at La Mojonera, we observed a spatial disassociation between beech seedlings and the diameter at breast height of trees excluding *Fagus* ( $X_k = -0.3$ ;  $P = 0.997$ ; Fig. 2(1A+D)). For Medio Monte, we also found a spatial disassociation between beech seedlings and mature trees of other species ( $X = -0.3$ ;  $P = 0.999$ ; Fig. 2(2A+D)).

The spatial patterns of association do not include cases of non-significant associations or disassociations. It also shows the distribution of significant clustering values ( $v_i$ ) ( $> 1.5 =$  patches;  $< -1.5 =$  gaps), and values obtained for the association index ( $X_k$ ) ( $> 0.5 =$  association;  $< -0.5$  disassociation).

## 4 Discussion

This is the first work that study spatial seedling patterns after a masting event in Mexican beech forest. The use of SADIE allowed us to detect spatial patterns of Mexican beech seedlings at specific locations and determine its association/disassociation with light availability and the presence of adult trees within the forest. The spatial indices obtained with SADIE showed that the distribution of adult beech trees favors the establishment and development of beech seedlings. We suggest that beech mother trees offer sheltering effect to the seedlings and saplings as suggested by Gorzelak et al. (2015). The Janzen–Connell hypothesis explains the maintenance of tropical tree diversity through the interacting effects of parent-centered dispersal patterns and distance- and density-dependent seed survival (Connell et al. 1984). When a gap is opened by fall of a conspecific tree, the opportunity emerges for the sapling to develop. Notwithstanding, the availability of suitable habitat for beech seedlings appears to be affected by the degree of canopy openness and the presence of several oak species (i.e., *Quercus delgadoana*, *Q. trinitatis*, and *Q. meavei*) and *Magnolia schiedeana* (Fig. 2(1A+D) and (2A+D)).

The possibility of changing spatial patterns (i.e., canopy openness) and its effects on the distribution of beech seedlings and saplings within forest stands requires further attention. Additional specific studies about beech seedlings, micro-environmental characteristics (i.e., pH, moisture, ectomycorrhizal, amount litter, stress, and allelopathy), adaptation of leaf morphology, and asymmetric competition for light resources are needed to understand recruitment and to clarify the influence of these features for the maintenance and dynamics of Mexican beech forests.



**Fig. 2** Maps of interpolated clustering and spatial association of Mexican beech seedling (A), canopy openness (B), and average diameter at breast height for different tree species: beeches (C) and other tree species (D), in two Mexican beech forests (1 = La Mojonera and 2 = Medio Monte).

Association is represented by two letters (i.e., A+B). Only significant indices were mapped:  $v_i > 1.5$  (patches) and  $v_i < -1.5$  (gaps) for aggregation;  $X_k > 0.5$  (positive aggregation) or  $X_k < 0.5$  (disassociation)

The distribution of seedlings may be a direct consequence of beechnut dispersal, which tends to be disseminated relatively close to the mother tree. Under the hypothesis, recruitment only occurs under a small “population recruitment curve” (Janzen 1970) that is centered at some distance from mother trees; this is possibly reflecting in the Mexican beech forests. Likewise, more field studies on the behavior of predatory animals (i.e., mammals, birds, snails, and insects) in relation to the spatial dispersal of beechnuts and Mexican beech seedlings are necessary.

Rodríguez-Ramírez et al. (2016) considered that Mexican beech is a species specialized in micro-environmental conditions within the Tropical Montane Cloud Forest. Besides, Akaji et al. (2016), Alvarez-Aquino et al. (2004), and

Camacho-Cruz et al. (2000) showed that the natural recruitment and survival of beech seedlings were higher within structurally mature forests than in more disturbed forests. Thus, despite the high mortality of beech seedlings and presence of conspecific trees, the high production of beechnuts during masting events appears to be enough for the maintenance of Mexican beech populations (Godínez-Ibarra et al. 2007; Cleavitt et al. 2008; Meyer and Pendleton 2015).

The observed relationship between diameter at breast height of mature trees and the spatial distribution of beech seedlings hotspots indicates that the presence of similar structure and floristic composition between Mexican beech stands studied (Rodríguez-Ramírez et al. 2016) is crucial for the establishment and survival of juveniles, providing

**Table 2** Spatial patterns of Mexican beech seedlings, canopy openness (CO), and dbh trees in two Mexican beech forests

Stand		$I_a$	$P$	$P_a$	$v_i$
La Mojonera	Beech seedlings	2.028	0.0002	-2.203	2.269
	Canopy openness	1.751	0.0005	-1.667	1.728
	dbh beech trees	2.051	0.0002	-2.1	2.113
	dbh neighboring tree species	2.338	0.0002	-2.293	2.396
Medio Monte	Beech seedlings	2.062	0.0002	-1.777	1.906
	Canopy openness	1.386	0.0183	-1.305	1.426
	dbh beech trees	2.424	0.0002	-2.075	2.289
	dbh neighboring tree species	1.247	0.0630	-1.199	1.29

$I_a$ , index of aggregation;  $I_a$ , 1 random pattern;  $I_a < 1$ , regular pattern;  $I_a > 1$  (italics), aggregated pattern;  $P_a > 0.975$ , regular dispersion;  $P < 0.025$ , (italics) spatial aggregation;  $v_i$ , mean of the index of clustering for patches

protection during the first developmental stages. Similarly, Čater and Kobler (2017), Collin et al. (2017), and Ohkubo et al. (1996) observed that the spatial distribution of individuals of *Fagus grandifolia* Ehrh., *F. sylvatica* L., and *F. japonica* Maxim. was positively associated with low levels of canopy openness.

We observed a similar association between the distribution of beech seedlings, canopy openness, and the conspecific trees within the two study sites. This suggests that the spatial distribution of beech seedlings is tightly linked to microsites with specific levels of light availability (Nelson and Wagner 2014; Peterson et al. 1990). In general, *Fagus*-dominated forests throughout the world have dense canopies ( $\approx 90\%$ ; Ishida et al. 2015; Yan et al. 2015), which favors the establishment and growth of beech seedlings. Several studies on the distribution and establishment of seedlings have shown similar results to ours by analyzing other beech species, namely *Fagus sylvatica* in southeastern Europe (Čater and Kobler 2017; Dusan et al. 2007), *F. crenata* Blume and *F. japonica* in Japan (Ariya et al. 2015; Ohkubo et al. 1996; Tomita et al. 2002), and *F. engleriana* Seemen in central China (Zhang et al. 2007). Similar patterns have also been observed in other tree species sharing environmental conditions with Mexican beech, such as *Magnolia schiedeana* and *M. dealbata* Zucc. in the Tropical Montane Cloud Forest of eastern Mexico (Dieringer and Espinosa 1994; Rivers et al. 2016; Vovides and Iglesias 1996). These shared patterns reinforce the importance of low levels of light availability to the germination and survival of non-light demanding tree species.

The present study advances our understanding of the processes involved in the natural recruitment of this highly endangered species with a relict distribution. However, the presence of oak species (i.e., *Quercus delgadoana*, *Q. trinitatis*, and *Q. meavei*) and *Magnolia schiedeana* in the surroundings and the differences in the tree structure and composition between forests determine light level and soil conditions in the understory. (Gazol and Ibáñez 2010; Nilsson 1985; Peña et al. 2011; Kitabatake and Wada 2001; Yuan et al. 2011).

Spatial distribution patterns of plant species in Tropical Montane Cloud Forest may also be influenced by niche assembly and random dispersal assembly processes acting at both local and landscape scales (Peña et al. 2011). The establishment of beech seedlings appears to be mainly influenced by conspecific tree distribution, subsequently is also affected by the presence of another tree species that are co-dominant in the Mexican beech forest.

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