Ecology/Ecología

Biodiversity relationships in three structural components in a beech forest of *Fagus grandifolia* subsp. *mexicana*

Relaciones de la biodiversidad en tres componentes estructurales de un bosque de hayas de *Fagus grandifolia* subsp. *mexicana*

Karina Calva-Soto[1], Numa P. Pavón[1]*, Arturo Sánchez-González[1], Claudia E. Moreno[1], and Neptalí Ramírez-Marcial[2].

[1] Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Hidalgo, Hidalgo, México.
[2] Departamento de Conservación de la Biodiversidad. El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, México.

*Corresponding author: npavon@uaeh.edu.mx

ABSTRACT
Background: Human activities (*e.g.*, logging and grazing) have perturbed the few beech forests that persist in the Sierra Madre Oriental, Mexico. However, basic information about ecological relationship in beech forests are scarce.
Questions: How are the relationship among structural components in a forest with high dominance of *Fagus grandiflora* subsp. *mexicana*?
Species study: *Fagus grandiflora* subsp. *mexicana* an endangered tree species.
Study site and dates: During 2015-2016 in a beech forest of *Fagus grandiflora* subsp. *mexicana* in San Bartolo Tutotepec, Hidalgo, Mexico.
Methods: In four circular plots (11.28 m diameter), all tree species were recorded. For seed bank sampling five circular subplots were established in each plot. Two soil samples (50 × 50 cm, 5 cm deep) were collected and seedlings were recorded in five subplots (two meters in diameter) in each plot. All species of seeds, seedlings and trees were identified.
Results: Seed bank was composed of 32 species while 17 and 9 species were registered for seedlings and trees, respectively. *F. grandifolia* subsp. *mexicana* and *Quercus delgadoana* were abundant both in seedling bank and tree canopy. Species compositions among the three beech forest structural components were significantly different.
Conclusions: The relationship among structural components were low. *Quercus delgadoana* in a future scenario would replace *F. grandiflora* subsp. *mexicana* as the dominant species in the forest.
Keywords: Biodiversity, cloud forest, restoration ecology, Sierra Madre Oriental, succession.

RESUMEN
Antecedentes: Las actividades humanas (tala y pastoreo) han perturbado los pocos bosques de hayas que aún persisten en la Sierra Madre Oriental, México. Sin embargo, la información básica sobre las relaciones ecológicas en estos bosques es escasa.
Pregunta: ¿Cuál son las relaciones en la biodiversidad entre los componentes estructurales en un bosque con alto dominio de *Fagus grandiflora* subsp. *mexicana*.
Especie de estudio: *Fagus grandiflora* subsp. *mexicana* una especie arbórea en peligro de extinción.
Sitio y años de estudio: Durante 2015-2016 en un bosque de hayas de *Fagus grandiflora* subsp. *mexicana* en San Bartolo Tutotepec, Hidalgo, México.
Métodos: En cuatro parcelas circulares (11.28 m de diámetro) se registraron todas las especies de árboles. Para el muestreo del banco de semillas se recolectaron dos muestras de suelo (50 × 50 cm, 5 cm de profundidad) y se registraron los árboles juveniles en cinco parcelas secundarias (2 m de diámetro) dentro de cada parcela. Se identificaron todas las especies de semillas, juveniles y árboles.
Resultados: El banco de semillas tuvo 32 especies, mientras que 17 y 9 especies fueron registradas de plántulas y árboles, respectivamente. *Fagus grandifolia* subsp. *mexicana* y *Quercus delgadoana* fueron especies más abundantes tanto en el banco de juveniles como en el estrato arbóreo. Las composiciones de especies entre los tres componentes estructurales del bosque de haya fueron significativamente diferentes.
Conclusiones: Las relaciones entre los componentes estructurales del bosque fueron. *Quercus delgadoana* podría, en un escenario futuro, remplazar a *F. grandiflora* subsp. *mexicana* como la especie dominante del bosque.
Palabras clave: Biodiversidad, bosque de niebla, restauración ecológica, Sierra Madre Oriental, sucesión.

Tropical montane cloud forest, particularly in Mexico, have high tree diversity because of their tropical and boreal components; however, many species are threatened by human activities (González-Espinosa *et al.* 2011). Furthermore, climate change projections for 2080 estimate that 68 % of current Mexican tropical montane cloud forests could be lost, with high impacts for many endemic species (Ponce-Reyes *et al.* 2012). One of the endangered species is a Mexican beech, *Fagus grandifolia* Ehrh. subsp. *mexicana* (Martínez) A.E. Murray, which is notable because it has been reported in only 11 localities (1,400-2,000 m asl), all of them in the Sierra Madre Oriental. The total area of beech forest in the country is *ca.* 200 ha (Rodríguez-Ramírez *et al.* 2013), with evidence of considerable perturbation from firewood extraction and sheep grazing.

Several studies have been carried out in Mexican beech forest, examining distribution (Williams-Linera *et al.* 2003, Rodríguez-Ramírez *et al.* 2013), population structure (Ortiz-Quijano *et al.* 2016), plant diversity (Gutiérrez-Lozano *et al.* 2017), population genetics (Rowden *et al.* 2004), seed germination, seedling survival and growth (Álvarez-Aquino & Williams-Linera 2002). These studies highlight the urgent need for beech forest conservation and restoration. To achieve these goals, it is necessary to obtain basic information about factors that affect natural regeneration, such as patterns and processes in seed and seedling banks. In general, late successional tree species such as *Fagus grandifolia* Ehrh., *F. orientalis* Lipsky and *F. sylvatica* L., do not form seed bank (Houle 1994, Olano *et al.* 2002, Schmidt *et al.* 2009, Esmailzadeh *et al.* 2011). Nevertheless, these types of tree species have high mortality rates in their seedling and sapling stages (from competition or herbivory), and those that survive make up the shade tolerant seedling bank (Gonzalez *et al.* 2008, Bedoya-Patiño *et al.* 2010). Seed and seedling banks have an essential role in ecological succession because they are sources of germplasm for regenerating the structure and function of forest ecosystems (Antos *et al.* 2005, Thompson 2000). Thus, in practice, both seed and seedling banks are useful for restoration projects (Martínez-Ramos & García-Orth 2007, Walker *et al.* 2007).

Species composition in forests can be explained by the relationships among the pools of species of each structural components (*i.e.*, seed bank, seedling bank, and tree canopy), through an internal dynamic. Therefore, the process takes place within the community through feedback loops (Li *et al.* 2010), where many species are shared among forest components. However, the fragmentation process and human perturbation have affected the internal dynamic of the forest, inducing changes in the species composition. Recently, the effect of fragmentation in a rainforest on community composition was evaluated in seedling, sapling and tree components reporting lower seedling richness (number of genera per plot) in the smallest and most isolated fragments (Stride *et al.* 2018). Possibly, with a posterior increase in the abundance of species related to the disturbance (Rutledge 2003). Thus, a greater diversity of more light-requiring forest species occurred in small gaps than in sites without disturbance in a beech forest (Degen *et al.* 2005). The above could be go-

ing through because it facilitates the entry of seeds, mainly herbs, from nearby disturbed sites such as pasturelands and agricultural areas, active or abandoned. On the other hand, the diversity of seedling is higher under canopy with greater tree-layer diversity in a beech-oak forest, while that in *Fagus sylvatica* forest the herb-layer was principally dominated by juvenile beech (Dölle *et al.* 2017). Thus, it would be expected that in conserved forests the relationship in biodiversity among structural components would be higher than in those disturbed by human activities within anthropized landscapes. Mexican beech forests fragments usually are small, surrounded by agricultural and livestock areas. In addition, they suffer disturbance due to logging, grazing, and in some cases, the beech´s seeds were collected for human consumption. The above, could generate a negative effect on the dynamics within the forest, affecting for example the abundance of beech seedling. The objective of this study was to analyze the relationship among seed bank, seedling and tree canopy in a beech forest, considering their alfa and beta diversity.

Materials and methods

Study area. Field sampling was carried out in a beech forest located in the south-central zone of the Sierra Madre Oriental (20° 36' - 20° 18' N and 98° 03' - 98° 20' W; 2,150 m asl, Figure 1). Livestock and agriculture are the two main land uses in the area (INEGI 2009). The climate is humid with temperatures between 9 and 16 °C, and 1,200 mm of annual rainfall. The forest is on regosol soil type and a 40º slope. In the site, the beeches are between 100 to 171 years old (Ortiz-Quijano *et al.* 2016). The forest was considered as beech forest because *F. grandiflora* subsp. *mexicana* was the most important species with 53.5 % of tree canopy abundances. Other canopy tree species were *Magnolia schiedeana* Schlecht ., *Quercus delgadoana* S. Valencia, Nixon & L.M. Kelly, *Symplocos limoncillo* Bonpl., and *Ostrya virginiana* K. Koch (Rodríguez-Ramírez *et al.* 2013). Abundant shrub species are *Eugenia capuli* Schltdl., *Ocotea klotzschiana* Hemsl., *Symplocos coccinea* Bonpl., and *Miconia glaberrima* Naudin (Ortiz-Quijano *et al.* 2016).

Sampling design. Four circular plots de 11.28 m diameter (based on the National Forestry Inventory) (CONAFOR 2012; Figure 1) in the beech forest were established. Tree cover was measured in each plot using a densitometer. We recorded all tree species with a diameter at breast height ≥ 10 cm. For seed bank sampling, another five circular subplots (two meters in diameter) were established in each plot (Figure 1). Two soil samples (50 × 50 cm and 5 cm deep) were collected from each subplot. Seeds in each sample were hand-picked, and grouped by color, shape and testa type (Van der Valk *et al.* 1992). After this, in order to register the very small seeds, soil samples were placed in greenhouse conditions (August 2015 - January 2016) to promote germination and seedling emergence. Determination of species was realized using seedling and expert support.

In each subplot, the naturally established seedlings were recorded and marked in two 50 × 50 cm areas. All seedling
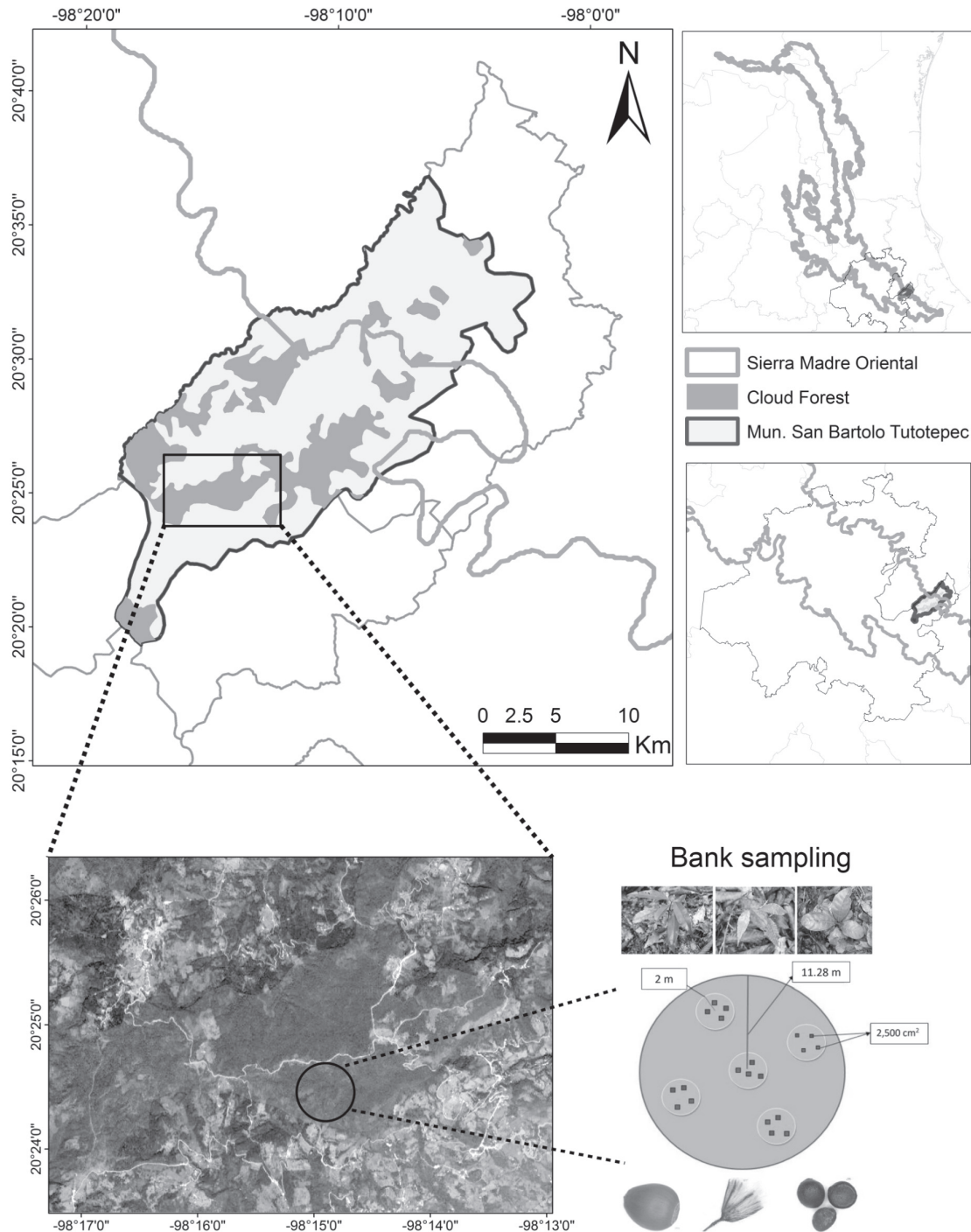
Figure 1. Location of the beech forest of San Bartolo Tutotepec, Hidalgo, Mexico. In the lower part, the satellite image and the sampling design were included.

species were identified using taxonomic keys and comparing them with live plants previously determined into the forest. Plant survival was recorded from February 2015 to January 2016. Abundance was estimated as the total number of seeds or seedling by species.

Data analysis. Biodiversity was estimated using abundance values to calculated species richness as Shannon index modified by Jost (2006) with the exponential order 1. Inventory completeness was calculated using species abundances to obtain the percentage of total individuals in the community

that were represented in the sample (Chao & Jost 2012). Rank-abundance graphs were also constructed to evenness analyzes.

In order to evaluate relationship among structural components (seed bank - seedling bank, seed bank - tree canopy and seedling bank - tree canopy), we first calculated Bray-Curtis dissimilarity indexes between pairs of samples using species abundances data. The Bray-Curtis index is widely used to generate distance matrices in vegetation ordination studies (Gotelli & Ellison 2004) and is very robust measure when sampling fractions are equal (Chao *et al*. 2006), as is shown here with the sample coverage (see results).

Then a permutational multivariate analysis of variance (PERMANOVA) was performed to compare differences between indices of each pair of structural components. PERMANOVA was realized with the 'vegan' package in R using the "adonis" function (Oksanen *et al*. 2017, R Core Team 2017).

Also, canopy cover was correlated with seed and seedling abundance using Spearman rank correlation analyses. In addition, we classified species according to their successional affinities, life forms, and dispersal types. Successional af-

finities were pioneer species (shade intolerant), secondary species (with fast growth and light shade tolerant), secondary-late species (shade tolerant with seed germination under canopy), and late or climax species (highly shade tolerant) (Rozza *et al*. 2007).

Results

Seed bank. A total 1,388 seeds were recorded from 32 species, 29 genera, 16 families, and seven undetermined morph-species; this inventory was 99 % of completeness according to the sample coverage. Asteraceae was the most abundant family, with 44.2 % of the total number of seeds. The seed bank was low evenness (Figure 2A). Four species had high abundance values, mainly *Coreopsis* sp., an early secondary species. In general, herbs were most abundant (44 %), followed by shrubs (36 %), trees (11 %), and vines (8 %) (Table 1). The most representative successional affinities were pioneer species (43 %) and early secondary species (36 %), while only 2.5 % were late successional species. Anemochory (46 %) and zoochory (43 %) were the most representative dispersal types. Two species, *Cotula* aff.
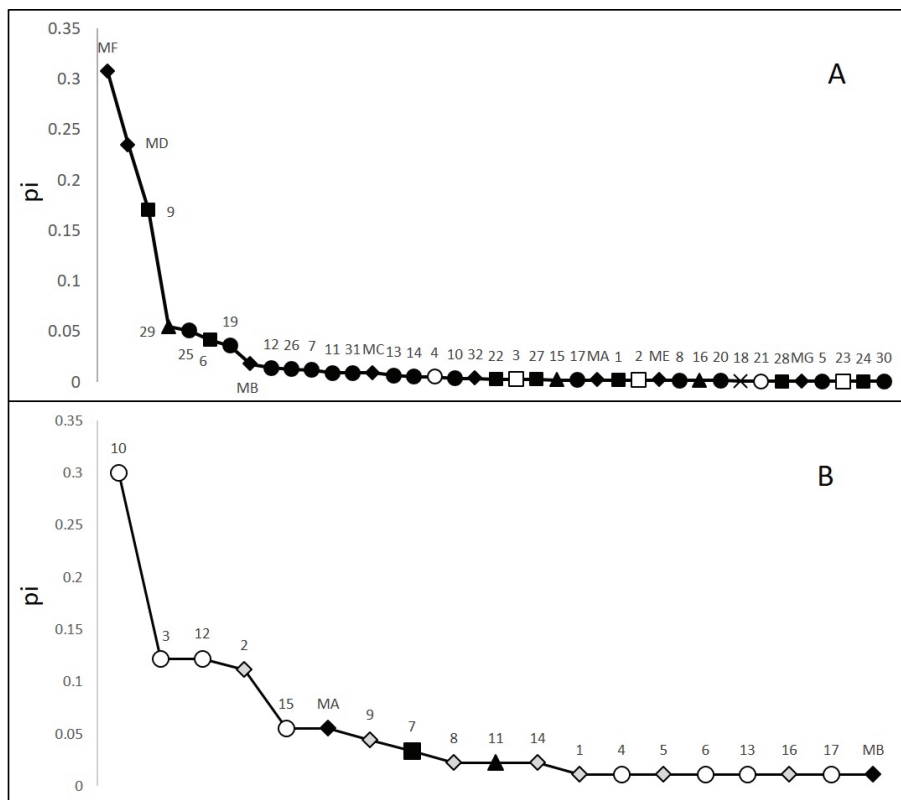

Figure 2. Rank-abundance curves of the species present in the seed bank (A) and seedling bank (B). Black circles indicate pioneer species, black squares early secondary species, white circles intermediate secondary species, gray diamonds late-successional species; black triangles represent species found in early and early secondary affinities, white squares indicate intermediate and secondary-late affinities. The crosses represent species of both initial and late secondary affinities. Black diamonds indicate morph-species. Numbers in the figures represent the species (see Tabla1) and M= morphospecies.

Table 1. Species registered in Mexicana beech forest. Structural components: SB = seed bank, SeB = seedling bank, TC = tree canopy. Life forms: T= Tree, Sh=Shrub, HA= Annual herbaceous, HAB= Annual or biennial herbaceous, HP= Perennial herbaceous, L= liana. Successional affinity: Pi= Pioneer, SI= Initial secondary, ST= Intermediate Secondary, LS= Late successional. Distribution: N= native, I= invasive. Dispersal type: A= Anemochory, B= Barochory, H= Hydrochory, Z= Zoochory, M= Anthropochory.

No.	Family/Species	Structural component	Lifeform	Successional affinity	Dispersion syndrome	Density (ind/m²)
	Acanthaceae					
1	*Thunbergia fragrans*	SB	HP	SI	H, M	0.06
	Adoxaceae					
2	*Viburnum* sp.	SB	T, Sh	SI, ST	Z	0.06
	Anacardiaceae					
3	*Rhus* sp.	SB	T, Sh	SI, ST	Z	0.08
	Apocynaceae					
4	*Thevetia* sp.	SB	T, Sh	ST	Z	0.14
	Araceae					
5	*Syngonium podophyllum*	SB	L	Pi	Z	0.02
	Asteraceae					
6	*Ageratina* sp.	SB	Sh	SI	A	1.12
7	*Baccharis conferta*	SB	Sh	Pi	A	0.32
8	*Chromolaena* aff. *collina*	SB	Sh	Pi	A	0.04
9	*Coreopsis* sp.	SB	Sh	SI	A	4.56
10	*Cotula* aff. *australis*	SB	HA	Pi	A	0.1
11	*Erigeron karvinskianus*	SB	HP	Pi	A	0.24
12	*Gamochaeta americana*	SB	HA	PI	A	0.38
13	*Mikania micrantha*	SB	Be	Pi	A	0.18
14	*Piqueria trinervia*	SB	HP	Pi	A	0.14
15	*Pseudognaphalium jaliscense*	SB	HP	Pi-SI	A	0.06
16	*Pseudognaphalium ehrenbergianum*	SB	HP	Pi-SI	A	0.04
17	*Pseudelephantopus spicatus*	SB	HA	Pi	A	0.06
18	*Roldana albonervia*	SB	Sh	SI-LS	A	0.02
19	*Simsia amplexicaulis*	SB	HA	Pi	Z	0.96
20	*Sinclairia deppeana*	SB	Sh	Pi	-	0.04
21	*Verbesina microptera*	SB	HA	ST	A	0.02
	Clethraceae					
	Clethra macrophylla	TC	T	LS	Z	-
	Commelinaceae					
22	*Commelina* sp.	SB	HP	SI	A	0.08
	Ericaceae					
33	*Vaccinium leucanthum*	SdB	T	LS	Z	0.1
	Fagaceae					
34	*Fagus grandifolia* subsp. *mexicana*	SdB, CT	T	LS	B, Z	1
23	*Quercus* sp.	SB	T	SI, ST	B, Z	0.02
35	*Quercus conspersa*	CT	T	LS	B, Z	-
36	*Quercus corrugata*	CT	T	LS	B, Z	-
	Quercus delgadoana	SdB, CT	T	ST	-	1.1
	Quercus meavei	SdB, CT	T	-	B, Z	1.1
	Lauraceae					
37	*Cinnamomum pachypodum*	SdB	T-Sh	LS	Z	0.1
38	*Litsea glaucescens*	SdB	Sh	ST	Z	0.1
39	*Nectandra salicifolia*	SdB	T	SI	Z	0.3
40	*Ocotea klotzschiana*	SdB, CT	T	LS	Z	0.2
	Linaceae					
24	*Linum nelsonii*	SB	HP, HA	Pi	Z	0.02
	Magnoliaceae					
41	*Magnolia schiedeana*	SdB, CT	T	LS	Z	0.4
	Melastomataceae					
42	*Miconia glaberrima*	SdB	Sh	ST	Z	2.7

Table 1. Continue.

No.	Family/Species	Structural component	Lifeform	Successional affinity	Dispersion syndrome	Density (ind/m²)
	Myrtaceae					
43	*Eugenia capuli*	SdB, CT	T	Pi-SI	Z	0.2
	Pentaphylacaceae					
44	*Cleyera theaeoides*	SdB	T	ST	-	1.1
45	*Ternstroemia sylvatica*	SdB	T	ST	Z	0.1
	Phytolaccaceae					
25	*Phytolacca rivinoides*	SB	Sh	Pi	Z	1.36
	Poaceae					
26	*Poa annua*	SB	HA	Pi	Z	0.34
	Polygalaceae					
27	*Monnina* sp.	SB	Sh	SI	Z	0.08
28	*Monnina xalapensis*	SB	Sh	SI	Z	0.02
	Primulaceae					
46	*Cybianthus* sp.	SdB	Sh	LS	Z	0.2
47	*Gaultheria acuminata*	SdB	Sh	ST	Z	0.5
	Rosaceae					
48	*Prunus samydoides*	SdB	T	LS	Z	0.1
49	*Rubus adenotrichos*	SdB	L	ST	Z	0.1
29	*Rubus* sp.	SB	Sh, Be	SI, ST	Z	1.46
	Rubiaceae					
30	*Coccocypselum hirsutum* var. *hirsutum*	SB	HP	SI	Z	0.02
	Solanaceae					
31	*Solanum myriacanthum*	SB	HA	Pi	Z	0.24
	Verbenaceae					
32	Verbenaceae sp1	SB	-	-	-	0.1

australis and *Poa annua* L., were alien species (Table 1). On the other hand, the canopy cover was not correlated with seed abundance ($r_s = -0.80$, $p = 0.083$).

Seedling bank. Seedlings of 17 species, 16 genera, nine families, and two morph-species were recorded. Lauraceae (23.5 %) and Fagaceae (17.6 %) were the families with the most species. The inventory completeness was 91 %. Species diversity was 10.41 effective species, and the most abundant were *M. glaberrima*, *Q. delgadoana*, *Cleyera theaeoides* (Sw.) Choisy, and *F. grandifolia* subsp. *mexicana*. Rank-abundance curves showed higher evenness than in the seed bank (Figure 2 B). The majority of seedlings were of secondary-late and late species (83 %). Trees were the most abundant life form (72 %), followed by shrubby species (22 %). Zoochory was the most common dispersal type with 84.2 % of the total number of species (Table 1).

Some species included in the seedling bank also were important components of the canopy; namely *F. grandifolia* subsp. *mexicana*, *E. capuli*, *M. scheideana*, *O. klotzschiana*, *Quercus delgadoana*, and *Q. meavei* Valencia-A., Sabás & Soto. Canopy cover was not correlated with seedling abundance values ($r_s = -0.015$, $p = 0.93$). Seedling survival was high in almost all species (> 80 %), with exception of the late secondary species *O. klotzschiana* and *Vaccinium leucanthum* Schltdl.

Tree canopy composition. Nine species and 1.6 true species were calculated in the tree canopy. Species with the highest abundance were *F. grandifolia* subsp. *mexicana* (53.5 %), *Q. delgadoana* (17.1 %), *E. capuli* (6.3 %), *M. scheideana* (5.5 %), *O. klotzschiana* (5.5 %), *Q. meavei* (3.5 %), *Q. aff. conspersa* (3.2 %), *Clethra macrophylla* M. Martens & Galeotti (2.5 %), and *Q. corrugata* Hook. (2.5 %) (Table 1). Canopy species were barely represented in the seed bank (one species) and seedling bank (six species), while only one species was shared with both banks.

Dissimilarity among structural components. Dissimilarity Bray Curtis indexes between seed bank and the seedling bank was 0.997 (S.D. = 0.005), between seed bank and tree canopy was 0.998 (S.D. = 0.005), and between the seedling bank and tree canopy was 0.792 (S.D. = 0.132). Consequently, species compositions among the three beech forest structural components were significantly different (Pseudo-*F* = 5.59, *p* < 0.001).

Discussion

Seed bank was dominated by herbs (pioneers), as has been reported in other beech forests (Williams-Linera 1993, Álvarez-Aquino *et al.* 2005, Ortiz-Arroña *et al.* 2008, Schmidt *et al.* 2009). This pattern could be the consequence of the

reproductive strategies of herbs; small seeds, anemochorous seed dispersal, high seed dormancy, fast growth, and short life history (Dalling 2002). In a *F. sylvatica* forest, herbs with anemochorous seed dispersal dominated the seed bank (Schmidt *et al*. 2009). Gaps within forest facilitate the entrance of seeds with anemochorous dispersal (Degen *et al*. 2005), and human disturbance increases the formation of gaps**.** Moreover, the presence of highly perturbed sites nearby favors the entry of herb seeds into the forest (Álvarez-Buylla & Martínez-Ramos 1994, Ramírez-Marcial *et al*. 1992).

The seed bank is a source of germplasm for starting secondary succession following extraordinary events that provoke tree canopy loss (Lavorel 1999). Some authors (Quintana-Ascencio *et al*. 1996, Dougall & Dodd 1997, Bossuyt *et al*. 2002, Álvarez-Aquino *et al*. 2005) have reported that a poor seed bank with low richness could be an indicator of good conditions, similar to found in mature or climax forest. Usually pioneer herbs have low seed dormancy (less than two years); consequently, the seed bank has continuous seed turnover due to seed dispersion (Álvarez-Buylla & Martínez-Ramos 1990, Salazar *et al*. 2011, EPPO 2016). We found very few tree seeds; these are more prone to predation because they have significant nutrient contents (Dalling 2002). On other Mexican forest insects predated 29 % of beech seeds (Godínez-Ibarra *et al*. 2007).

Seedling bank was dominated by trees (secondary-late and late species). This composition is a good indicator of the potential for forest regeneration (Lavorel 1999, Brang 2001, Bedoya-Patiño *et al*. 2010). Similar results were reported in a *F. crenata* Blume forest with 20 species in its seedling bank (Hara 1987). We estimated a lower seedling density (one seedling per m²) compared to other Mexican beech forests with 3.2 seedlings per m² (Álvarez-Aquino & Williams-Linera 2002). It is possible that direct perturbation consisting of seeds gathered for food by local inhabitants (Ortiz-Quijano *et al*. 2016) could be having an adverse effect on seedling recruitment. Furthermore, animals could eat early seedlings, for example, rodents consumed *F. crenata* seedlings (Abe *et al*. 2005).

Old records have shown that primary beech forests had high tree canopy diversity. Lutz (1930) reported 32 tree species in a forest in Pennsylvania at the beginning of the nineteenth century. However, only six tree species constituted 88 % of the stand, and *F. grandifolia* represented 30.8 % of the total abundance. In the beech forest studied, two species together account for 70.6 % of the tree abundance, *F. grandifolia* (53.5 %) and *Q. delgadoana* (17.1 %); although they coexist with 19 other canopy species. Thus, not all beech forest are monospecific, even in central Germany, there are a beech forests of *F. sylvatica* shares dominance with another three to six canopy tree species (Schmidt *et al*. 2009). Worldwide distribution of beech forest is restricted to specific ecological conditions, but its dominance may be a consequence of its capacity to create suitable environmental conditions (Pignatti *et al*. 2006). Many factors could explain the differences in tree canopy richness, such as the age of the stand, natural or anthropic perturbation, and climate conditions (Cao 1995, Cao & Peters 1997, Shen *et al*. 2015). In

particular, human activities have a large impact; logging of the surrounding area and within the beech forest fragment, grazing, and beech seed extraction could change environmental conditions to favor other competitive species such as *Q. delgadoana*. The presence of species indicative of perturbation in the beech forest such as *Baccharis conferta* Kunth and *Phytolacca rivinoides* Kunth & C.D. Bouché, and the alien species *Cotula* aff. *australis* and *P. annua*, could be evidence of such changes (Díaz & Elcoro 2009, Martínez-Orea *et al*. 2013).

The relationships among the seed bank, seedling bank, and tree canopy in beech forest have been little explored. Most published studies have examined only one or two components (Houle 1994, Hopfensperger 2007, Esmailzadeh *et al*. 2011). Schmidt *et al*. (2009) reported a positive correlation between tree canopy richness and seed bank richness in temperate broad-leaved forests. However, this relationship was not found in the present study; rather, differences between seed bank and tree canopy were expected because different ecological succession processes are operating in different stages, with floristic turnover between stages (Grime 2006). Low floristic similarity among structural components has occurred in other beech forests (Olano *et al*. 2002, Schmidt *et al*. 2009). A meta-analysis using data from different types of forest showed a low floristic similarity (31%) between the seed bank and tree canopy, with only three studies with values lower than 10 % (Hopfensperger 2007). On the other hand, significant differences between a seedling bank and tree canopy are uncommon, considering that the seedling bank is a source for canopy renewal. High seedling survival suggests that shade tolerant plants can stay alive for several years (Gonzalez *et al*. 2008, Bedoya-Patiño *et al*. 2010); beech is an excellent example of a shade tolerant plant species (Nagel *et al*. 2010, Kuninaga *et al*. 2015). It has been reported that 92 % of *F. grandifolia* subsp. *mexicana* seedlings survive for at least 18 months (Álvarez-Aquino & Williams-Linera 2002). However, mortality increases significantly when the seedlings become juvenile trees, so this is a critical step for species regeneration (Collet *et al*. 2011, Kuninaga *et al*. 2015).

Gap dynamics are a key factor in beech forest regeneration because light reaches the forest floor and allows *Fagus* seedling growth (Peters & Platt 1996, Degen *et al*. 2005). In *F. crenata* forests, light also causes stem thickening in juvenile plants, and this could be a competitive advantage over other plant species (Abe *et al*. 2005, Kuninaga *et al*. 2015). *F. sylvatica* seedlings had greater success for gap regeneration than other canopy species such as *Acer campestre* L., *A. platanoides* L., *Carpinus betulus* L., or *Fraxinus excelsior* L. (Collet *et al*. 2008). However, beech species could be replaced by other canopy species; for example, *Abies*, *Acer*, and *Betula*, that can take the place of *F. sylvatica* and *F. crenata* (Peters & Platt 1996, Waltert *et al*. 2002, Abe *et al*. 2005, Nagel *et al*. 2010). Greater physiological plasticity has been reported in *Q. robur* seedlings than in those of *F. sylvatica*, with a better photosynthetic response to light (Valladares *et al*. 2002), which could be interpreted as a competitive advantage in gaps. This may explain, at least

partly, that beech regeneration was negatively correlated with canopy openness (Barna & Bosela 2015). Besides, the beech regeneration was negatively correlated with canopy openness. For above is possibly that the forest studied could be a beech-oak forest (*F. grandiflora* subsp. *mexicana* and *Q. delgadoana*) with particular process to coexistence, as other similar European forest (Dölle *et al.* 2017). On the other hand, if human perturbation continues, together with climate change, *Q. delgadoana* could replace *F. grandifolia* subsp., *mexicana*, because the oak species was the second most important canopy tree, with the highest seedling density and is the dominant species in the adjacent oak forest. Replacement patterns of beech by others dominant species has been reported in other forest (Poulson & Platt 1996, Forrester & Runkle 2000, Peñuelas *et al.* 2007).

Acknowledgments

Literature cited

Abe M, Miguchi H, Honda A, Makita A, Nakashizuka T. 2005. Short-term changes affecting regeneration of *Fagus crenata* after the simultaneous death of *Sasa kurilensis*. *Journal of Vegetation Science* 16: 49-56.
DOI: https://doi.org/10.1111/j.1654-1103.2005.tb02337.x

Álvarez-Aquino C, Williams-Linera G. 2002. Seedling bank dynamics of Fagus grandifolia var. mexicana before and after a mast year in a Mexican cloud forest. *Journal of Vegetation Science* 13: 179-184.
DOI: https://doi.org/10.1111/j.1654-1103.2002.tb02037.x

Álvarez Aquino C, Williams Linera G, Newton AC. 2005. Disturbance effects on the seed bank of mexican cloud forest fragments. *Biotropica* 37: 337-342.
DOI: https://doi.org/10.1111/j.1744-7429.2005.00044.x

Álvarez-Buylla ER, Martínez-Ramos M. 1990. Seed bank versus seed rain in the regeneration of a tropical pioneer tree. *Oecologia* 84: 314-325.
DOI: https://doi.org/10.1007/BF00329755

Antos JA, Guest HJ, Parish R. 2005. The tree seedling bank in an ancient montane forest: stress tolerators in a productive habitat. *Journal of Ecology* 93:536-543.
DOI: https://doi.org/10.1111/j.1365-2745.2005.00968.x

Barna M, Bosela M. 2015. Tree species diversity change in natural regeneration of a beech forest under different management. *Forest Ecology and Management* 342: 93-102. DOI: https://doi.org/10.1016/j.foreco.2015.01.017

Bedoya-Patiño JG, Estévez-Varón JV, Castaño-Villa GJ. 2010. Banco de semillas del suelo y su papel en la recuperación de los bosques tropicales. *Museo de Historia Natural* 14: 77-91.

Bossuyt B, Heyn M, Hermy M. 2002. Seed bank and vegetation composition of forest stands of varying age in central Belgium: consequences for regeneration of ancient forest vegetation. *Plant Ecology* 162: 33-48.
DOI: https://doi.org/10.1023/A:1020391430072

Brang P. 2001. Resistance and elasticity: promising concepts for the management of protection forests in the European Alps. *Forest Ecology and Management* 145: 107-119. DOI: https://doi.org/10.1016/s0378-1127(00)00578-8

Cao KF. 1995. *Fagus dominance in Chinese montane forests: natural regeneration of Fagus lucida and Fagus hayatae var. pashanica*. China: Wageningen, Agricultural University. ISBN: 90-5485-330-1; ISBN 9789054853305

Cao KF, Peters R. 1997. Species diversity of Chinese beech forests in relation to warmth and climatic disturbances. *Ecological Research* 12: 175-189.
DOI: https://doi.org/10.1007/BF02523783

Chao A, Chazdon RL, Colwell RK, Shen TJ. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62: 361-371. DOI: https://doi.org/10.1111/j.1541-0420.2005.00489.x

Chao A, Jost L. 2012. Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology* 93: 2533-2547.
DOI: https://doi.org/10.1890/11-1952.1

Collet C, Piboule A, Leroy O, Frochot H. 2008. Advance *Fagus sylvatica* and *Acer pseudoplatanus* seedlings dominate tree regeneration in a mixed broadleaved former coppice-with-standards forest. *Forestry* 81:135-150.
DOI: https://doi.org/10.1093/forestry/cpn004

Collet C, Fournier M, Ningre F, Hounzandji API, Constant T. 2011. Growth and posture control strategies in *Fagus sylvatica* and *Acer pseudoplatanus* saplings in response to canopy disturbance. *Annals of Botany* 107: 1345-1353.
DOI: https://doi.org/10.1093/aob/mcr058

CONAFOR [Comisión Nacional Forestal]. 2012. Inventario Nacional Forestal y de Suelos, Informe 2004-2009. Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT), México. http://www.ccmss.org.mx/wp-content/uploads/2014/10/Inventario_nacional_forestal_y_de_suelos_informe_2004_-_2009_.pdf (accessed November 16, 2018).

Dalling JW. 2002. Ecología de semillas. *In*: Guariguata MR, Kattan GH. Eds. *Ecología y Conservación de Bosques Neotropicales*, p. 345-375, Costa Rica: Asociacion De Editoriales. ISBN-10: 9968801119; ISBN-13: 978-9968801119

Degen T, Devillez F, Jacquemart AL. 2005. Gaps promote plant diversity in beech forests (Luzulo-Fagetum), North Vosges, France. *Annals of Forest Science* 62: 429-440.
DOI: https://doi.org/10.1051/forest:2005039

Díaz WA, Elcoro S. 2009. Plantas colonizadoras en áreas perturbadas por la minería en el Estado Bolívar, Venezuela. *Acta Botánica Venezuelica* 32: 453-466.

Dölle M, Petritan AM, Biris IA, Petritan IC. 2017. Relations between tree canopy composition and understorey vegetation in a European beech-sessile oak old growth forest in Western Romania. *Biologia* 72: 1422-1430.
DOI: https://doi.org/10.1515/biolog-2017-0165

Dougall TAG, Dodd JC. 1997. A study of species richness and diversity in seed banks and its use for the environmental mitigation of a proposed holiday village development in a

coniferized woodland in south east England. *Biodiversity & Conservation* **6**: 1413-1428.
DOI: https://doi.org/10.1023/A:1018345915418

EPPO [European and Mediterranean Plant Protection Organization Global Database]. 2016. The situation of *Baccharis halimifolia* in the EPPO region. https://gd.eppo.int/ (accessed December 3, 2018).

Esmailzadeh O, Hosseini SM, Tabari M, Baskinb CC, Asadi H. 2011. Persistent soil seed banks and floristic diversity in *Fagus orientalis* forest communities in the Hyrcanian vegetation region of Iran. *Flora - Morphology, Distribution, Functional Ecology of Plants* **206**: 365-372.
DOI: https://doi.org/10.1016/j.flora.2010.04.024

Forrester JA, Runkle JR. 2000. Mortality and replacement patterns of an old-growth *Acer-Fagus* woods in the Holden Arboretum, northeastern Ohio. *The American Midland Naturalist* **144**: 227-243. DOI:
https://doi.org/10.1674/0003-0031(2000)144[0227:MARPOA]2.0.CO;2

Godínez-Ibarra O, Ángeles-Pérez G, López-Mata L, García-Moya E, Valdez-Hernández JI, de los Santos-Posadas H, Trinidad-Santos A. 2007. Seed rain and seedling emergence of *Fagus grandifolia* subsp. *mexicana* at La Mojonera, Hidalgo, Mexico. *Revista Mexicana de Biodiversidad* **78**: 117-128. DOI: http://dx.doi.org/10.22201/ib.20078706e.2007.001.394

González M, Deconchat M, Balent G, Cabanettes A. 2008. Diversity of woody plant seedling banks under closed canopy in fragmented coppice forests. *Annals of Forest Science* **65**: 511-511. DOI: https://doi.org/10.1051/forest:2008029

González-Espinosa M, Meave JA, Lorea-Hernández FG, Ibarra-Manríquez G, Newton AC. 2011. *The Red List of Mexican cloud forest trees*. Cambridge: Fauna y Flora International. ISBN: 9781903703281

Gotelli NJ, Ellison AM. 2004. *Primer of ecological statistics*. Sinauer Associates Publishers, Massachusetts, USA. ISBN: 9781605350646

Grime JP. 2006. *Plant Strategies, Vegetation Processes and Ecosystem Properties*, USA:. John Wiley & Sons, ISBN-10: 047085040X; ISBN-13: 978-0470850404

Gutiérrez-Lozano M, Sánchez-González A, López-Mata L, Tejero-Díez D. 2017. Taxonomic richness of lycophytes and ferns of the Mexican beech forest: Highest ever recorded among *Fagus* forests worldwide? *Flora* **229**: 23-31. DOI: https://doi.org/10.1016/j.flora.2017.02.008

Hara M. 1987. Analysis of seedling banks of a climax beech forest: ecological importance of seedling sprouts. *Vegetatio* **71**: 67-74.

Hopfensperger KN. 2007. A review of similarity between seed bank and standing vegetation across ecosystems. *Oikos* **116**: 1438-1448.
DOI: https://doi.org/10.1111/j.0030-1299.2007.15818.x

Houle G. 1994. Spatiotemporal patterns in the components of regeneration of four sympatric tree species–*Acer rubrum*, *A. saccharum*, *Betula alleghaniensis* and *Fagus grandifolia*. *Journal of Ecology* **82**: 39-53.

INEGI [Instituto Nacional de Estadística y Geografía]. 2009. Prontuario de información geográfica municipal de los Estados Unidos Mexicanos San Bartolo Tutotepec, Hidalgo Clave

geoestadística 13053 2009. <http://www3.inegi.org.mx/contenidos/app/mexicocifras/datos_geograficos/13/13053.pdf> (accessed July 2, 2019).

Jost L. 2006. Entropy and diversity. *Oikos* **113**: 363-375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Kuninaga T, Hirayama K, Sakimoto M. 2015. Negative canopy-understorey interaction shapes the sapling bank of *Fagus crenata* in a cool-temperate, conifer-hardwood mixed forest. *Plant Ecology* **216**: 1191-1202.
DOI: https://doi.org/10.1007/s11258-015-0501-9

Lavorel S. 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. *Diversity and Distribution* **5**: 3-13.
DOI: https://doi.org/10.1046/j.1472-4642.1999.00033.x

Li X, Liu W, Tang CQ. 2010. The role of the soil seed and seedling bank in the regeneration of diverse plant communities in the subtropical Ailao Mountains, Southwest China. *Ecological Research* **25**: 1171-1182.
DOI: https://doi.org/10.1007/s11284-010-0742-y

Lutz HJ. 1930. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. *Journal of Forestry* **28**: 1098-1103.
DOI: https://doi.org/10.1093/jof/28.8.1098

Martínez-Orea Y, Castillo-Argüero S, Álvarez-Sánchez J, Collazo-Ortega M, Zavala-Hurtado A. 2013. Lluvia y banco de semillas como facilitadores de la regeneración natural en un bosque templado de la ciudad de México. *Interciencia* **38**: 400-409.

Martínez-Ramos M. 1994. Regeneración natural y diversidad de especies arbóreas en selvas húmedas. *Boletín de la Sociedad Botánica de México* **54**: 179-24.
DOI: http://dx.doi.org/10.17129/botsci.1431

Martínez-Ramos M, García-Orth X. 2007. Sucesión ecológica y restauración de las selvas húmedas. *Boletín de la Sociedad Botánica de México* **80S**: 69-84.
DOI: http://dx.doi.org/10.17129/botsci.1758

Nagel TA, Svoboda M, Rugani T, Diaci J. 2010. Gap regeneration and replacement patterns in an old-growth *Fagus-Abies* forest of Bosnia-Herzegovina. *Plant Ecology* **208**: 307-318.
DOI: https://doi.org/10.1007/s11258-009-9707-z

Oksanen J, Guillaume F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens HMH, Szoecs E, Wagner H. 2017. Vegan: Community Ecology Package. R package version 2.4-3. https://CRAN.R-project.org/package=vegan (accessed January 23, 2013).

Olano JM, Caballero I, Laskurain NA, Loidi J, Escudero A. 2002. Seed bank spatial pattern in a temperate secondary forest. *Journal of Vegetation Science* **13**: 775-784.
DOI: https://doi.org/10.1111/j.1654-1103.2002.tb02107.x

Ortiz-Arroña A, Sánchez-Velásquez LR, Castillo BJ. 2008. Banco de semillas en el suelo de un bosque mesófilo de montaña en la Sierra de Manantlán, México. *Scientia-CUCBA* **10**: 81-94.

Ortiz-Quijano AB, Sánchez-González A, López-Mata L, Villanueva-Díaz J. 2016. Population structure of *Fagus grandifolia* subsp. *mexicana* in the cloud forest of Hidalgo State, Mexico. *Botanical Sciences* **94**: 483-497.
DOI: https://doi.org/10.17129/botsci.515

Peñuelas J, Ogaya R, Boada M, Jump A. 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography* **30**: 829-837.
DOI: https://doi.org/10.1111/j.2007.0906-7590.05247.x

Peters R, Platt WJ. 1996. Growth strategies of main trees and forest architecture of a *Fagus-Magnolia* forest in Florida, USA. *Vegetatio* **123**: 39-49.
DOI: https://doi.org/10.1007/BF00044886

Pignatti S, Cresta C, Testi A, Crosti R, Fukushima T, Maldonado SN. 2006. Comparative ecological investigations in *Fagus* forests of Japan, Italy and Mexico. *Rendiconti Lincei* **17**: 299-310. DOI: https://doi.org/10.1007/BF02904768

Ponce-Reyes R, Reynoso-Rosales VH, Watson JEM, VanderWal J, Fuller RA, Pressey RL, Possingham HP. 2012. Vulnerability of cloud forest reserves in Mexico to climate change. *Nature Climate Change* 2: 448-452. **2**: 1-5.
DOI: https://doi.org/10.1038/nclimate1453

Poulson TL, Platt WJ. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. *Ecology* **77:** 1234-1253. DOI: https://doi.org/10.2307/2265592

Quintana-Ascencio PF, Gonzalez-Espinosa M., Ramírez-Marcial N, Domínguez-Vazquez G, Martinez-Ico M. 1996. Soil seed banks and regeneration of tropical rain forest from milpa fields at the Selva Lacandona, Chiapas, Mexico. *Biotropica* **28**: 192-209. DOI: https://doi.org/10.2307/2389074

Ramírez-Marcial N, González-Espinoza M, Quintana-Ascencio PF. 1992. Banco y lluvia de semillas en comunidades sucesionales de bosques de pino-encino de los altos de Chiapas, México. *Acta Botánica Mexicana* **20**: 59-75.
DOI: https://doi.org/10.21829/abm20.1992.658

Rodríguez-Ramírez ECh, Sánchez-González A, Ángeles-Pérez G. 2013. Current distribution and coverage of Mexican forests *Fagus grandifolia* subsp. *mexicana* in Mexico. *Endangered Species Research* **20**: 205-216.
DOI: https://doi.org/10.3354/esr00498

Rowden A, Robertson A, Allnutt T, Heredia S, Williams-Linera G, Newton A. 2004. Conservation genetics of Mexican beech, *Fagus grandifolia* var. *mexicana*. *Conservation Genetics* **5**: 475-484.
DOI: https://doi.org/10.1023/B:COGE.0000041028.02423.c0

Rozza AF, Turini FF, Rodrigues RR. 2007. Ecological management of degraded forest fragments. *In*: Rodrigues RR, Martins SV, Gandolfi S. Eds. *High Diversity Forest Restoration in Degraded Areas*, Nueva York: Nova Science Publishing pp. 171-196. ISBN-10: 1600214215; ISBN-13: 978-1600214219

Rutledge DT 2003. *Landscape indices as measures of the effects of fragmentation: can pattern reflect process?* New Zealand: Department of Conservation. ISBN: 0-478-22380-3

Salazar A, Goldstein G, Franco AC, Miralles-Wilhelm F. 2011. Timing of seed dispersal and dormancy, rather than persistent soil seed-banks, control seedling recruitment of woody plants in Neotropical savannas. *Seed Science Research* **21**: 103-116.
DOI: https://doi.org/10.1017/S0960258510000413

Schmidt I, Leuschner C, Mölder A, Schmidt W. 2009. Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. *Forest Ecology and Management* **257**: 695-702.
DOI: https://doi.org/10.1016/j.foreco.2008.09.052

Shen ZH, Fang JY, Chiu CA, Chen TY. 2015. The geographical distribution and differentiation of Chinese beech forests and the association with *Quercus*. *Applied Vegetation Science* **18**: 23-33. DOI: https://doi.org/10.1111/avsc.12108

Stride G, Thomas CD, Benedick S, Hodgson JA, Jelling A, Senior MJ, Hill JK. 2018. Contrasting patterns of local richness of seedlings, saplings, and trees may have implications for regeneration in rainforest remnants. *Biotropica* **50**: 889-897.
DOI: https://doi.org/10.1111/btp.12605

R Core Team (2017). R: A language and environment for statistical computing. R Foundadion for. Statistical Computing, Vienna, Austria.

Thompson K. 2000. The functional ecology of soil seed banks. *In*: Fenner M. Ed. *Seeds: The Ecology of Regeneration in Plant Communities,* pp. 215-235, London: CABI Publishing. ISBN-10: 0851994326; ISBN-13: 978-0851994321

Valladares F, Chico J, Aranda I, Balaguer L, Dizengremel P, Manrique E, Dreyer E. 2002. The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees* **16**: 395-403. DOI: https://doi.org/10.1007/s00468-002-0184-4

Van der Valk AG, Pederson RL, Davis CB. 1992. Restoration and creation of freshwater wetlands using seed banks. *Wetlands Ecology and Management* **1**: 191-197.
DOI: https://doi.org/10.1007/BF00244924

Walker L, Walker J, del Moral R. 2007. Forging a new alliance between succession and restoration. *In*: Walker LR, Walker J, Hobbs RJ, eds. *Linking Restoration and Ecological Succession*, pp. 1-18, USA: Springer. ISBN-10: 038735302X; ISBN-13: 978-0387353029

Waltert B, Wiemken V, Rusterholz HP, Boller T, Baur B. 2002. Disturbance of forest by trampling: Effects on mycorrhizal roots of seedlings and mature trees of *Fagus sylvatica*. *Plant and Soil* **243**: 143-154.
DOI: https://doi.org/10.1023/A:1019983625473

Williams-Linera G. 1993. Soil seed banks in four lower montane forests of Mexico. *Journal of Tropical Ecology* **9**: 321-337.
DOI: https://doi.org/10.1017/S0266467400007379

Williams-Linera G, Rowden A, Newton AC. 2003. Distribution and stand characteristics of relict populations of Mexican beech (*Fagus grandifolia* var. *mexicana*). *Biological Conservation* **109**: 27-36.
DOI: https://doi.org/10.1016/S0006-3207(02)00129-5

Author contributions: KCS (https://orcid.org/0000-0003-4462-9516), and NPP (https://orcid.org/0000-0003-0666-5268) performed the data collection and data analysis. KCV, NPP, ASG (https://orcid.org/0000-0002-3190-8789), CEM (https://orcid.org/0000-0002-9584-2619), and NRM (https://orcid.org/0000-0003-1793-0178) were responsible for the study conception, design and drafting of the manuscript.