Regeneration patterns in Mexican pine-oak forests

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Abstract

Background: Global change is causing an increase in the incidence of natural and anthropogenic disturbances on forests, which frequently interact synergistically and promote changes in forest structure, composition and functioning. In this study we evaluate the regeneration of Pinaceae and Fagaceae species in pure and mixed stands in Mexico to determine if current regeneration patterns are indicative of changes in the relative dominance of these two tree families, as observed in other temperate regions. We also identify the environmental factors that determine the regeneration patterns of Pinaceae and Fagaceae species in these forests.

Results: We use data from two consecutive surveys of the National Inventory of Forests and Soils of Mexico (INFyS), obtained in 2004–2009 and 2009–2014. Our results show that the spatial patterns of regeneration are affected by forest structure, by climate, by the type and intensity of disturbances and by land tenure. Importantly, the presence and abundance of Fagaceae regeneration is generally higher than that of Pinaceae, and tends to be favoured (relative to Pinaceae) under warmer climates and by the presence of wildfires.

Conclusions: The higher regeneration of Fagaceae relative to Pinaceae under warmer and fire-prone conditions could have important impacts on the composition and functioning of Mexican temperate forests under ongoing climate change, as well as affect their resilience to future disturbances.

Keywords: Fagaceae, Forest dynamics, Forest inventory, Mexico, Pinaceae, Regeneration, Temperate forests

Background

Climate change is causing an increase in the incidence of disturbances such as drought, natural fires, pests and diseases (Brecka et al. 2018; Prǎvǎlie 2018), which can drive rapid changes in forests (Allen et al. 2015). Moreover, recent anthropogenic changes due to forest exploitation, extensive grazing and land use changes are also modifying the composition and structure of forest ecosystems (Burgi et al. 2000; Gimmi et al. 2010; Easterday et al. 2018). Examples include the increase of drought-tolerant and slow-growing species in tropical and temperate environments (Feeley et al. 2011; Allen et al. 2012; Zhang et al. 2018), substitution of late-successional by early-successional conifers caused by the increase in the frequency of fires associated with climate change (Carcaillet et al. 2001; Searle and Chen 2017) or the transition from conifers to broadleaf species in

temperate forests (Rigling et al. 2013; Vayreda et al. 2016; Alfaro-Reyna et al. 2018).

To understand and forecast shifts in forest composition, it is essential to characterize the regeneration patterns of tree species (cf. Martínez-Vilalta and Lloret 2016 for the specific case of drought-induced forest decline), including the conditions that allow the establishment and survival of new recruits of different species, as well as their response under different natural and anthropogenic disturbance regimes (Denslow 1980). Regeneration dynamics can be understood in terms of tolerance to limiting resources, such as the availability of water and nutrients or the exposure to light (Agyeman et al. 1999; Woodward et al. 2004). Shade-intolerant species tend to have a higher growth rate under direct light conditions and usually dominate the low canopies initially, but when canopies close they are typically replaced by species that tolerate more shaded conditions, at least in their early stages of development, which are usually classified as late-successional species (Swaine and Whitmore 1988).

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Temperate forest ecosystems occupy 26% of the world's forest cover and dominate large areas of the northern hemisphere (Keenan et al. 2015; Riitters et al. 2016). These forests are largely dominated by members of the Fagaceae and Pinaceae families. Many Pinaceae are characterized as being intolerant to shade and require open areas with little plant cover to establish (Ramírez-Marcial et al. 2001; Quintana-Ascencio et al. 2004; Coomes et al. 2005), although many exceptions exist (e.g. Stephens and Gill 2005; González-Tagle et al. 2008). Thus, in xeric environments, Pinaceae may require tree protection or nursery for the successful recruitment of seedlings (e.g. Gómez-Aparicio et al. 2004). Edaphic properties combined with water availability significantly influence the establishment of *Pinus* species (Barton 1993; Carnicer et al. 2014; Pompa-García et al. 2018). On the other hand, most Fagaceae are considered semi-tolerant to shade, as they can live under closed canopies during the juvenile and adult stages, although in the early stages of life light requirements are sometimes greater (Galindo-Jaimes et al. 2002; Berg et al. 2018). In general, oaks have a greater range of tolerance to drought than pines (Rigling et al. 2013; Montes-Hernández and López-Barrera 2013; Carnicer et al. 2014) and also have a high capacity of resprouting after a disturbance (Cooper et al. 2018). As a result, replacement of pine-dominated forests by oak woodlands and shrublands after large fires has been documented in recent decades in North America (Goforth and Minnich 2008; Barton and Poulos 2018) and Europe (Rodrigo et al. 2004). In addition, several studies have reported increased regeneration of oaks relative to pines in temperate forests where these two groups coexist, particularly under warm and dry conditions in Southern Europe (Vayreda et al. 2013; Carnicer et al. 2014).

Temperate forests of Mexico, due to their high diversity of pines and oaks, are considered a center of diversification of those groups (Challenger and Soberón 2008), hosting 61 species of Pinaceae (Gernandt and Pérez-de la Rosa 2014) and 125 species of Fagaceae (Valencia-A 2004; Valencia-A and Gual-Díaz 2014). The patterns of distribution of these forests reflect the historically common disturbances in the region, such as forest thinning and wood extractions, grazing and fires (Pompa-García et al. 2018). Several studies have analyzed the local regeneration patterns of pine-oak forests after different types of disturbances in Mexico (Galindo-Jaimes et al. 2002; Rodríguez-Trejo and Fulé 2003; Asbjornsen et al. 2004; López-Barrera and Newton 2005; González-Tagle et al. 2008). However, there is little information on the regeneration of both groups at a regional scale for different forest types and how it has been influenced by recent climate change.

In this study we analyze the patterns of Pinaceae and Fagaceae regeneration in Mexican forests using data from two consecutive surveys of the National Forest and Soil Inventory of Mexico (INFyS, CONAFOR 2015). Firstly, we evaluate the regeneration of Pinaceae and Fagaceae in forests with pure and mixed overstory to determine if current regeneration patterns are indicative of forest composition shifts, as observed in other temperate regions. Secondly, we identify the environmental factors that determine the regeneration patterns of pines and oaks in these forests. We hypothesize that Fagaceae will tend to regenerate better than Pinaceae in all forests where these two species groups coexist in the ovestory, and that this pattern will be exacerbated under warmer conditions and in areas subjected to intense and frequent disturbance regimes.

Materials and methods
Study area
The study area covers the whole distribution of pine, oak, and pine-oak forests in Mexico (between 86° and 117° W, and between 14° and 32° N) (Fig. 1), which are mainly distributed in the Sierra Madre Occidental, in the eastern slope of the Sierra Madre Oriental and in some parts of the southern mountain systems and the humid subtropical zone (Miranda and Hernández-X 1963; INEGI 2014). These forests are largely dominated by species of *Pinus*, *Quercus* or both. They are distributed mainly in regions of temperate and cold climates, rainy or subhumid with summer rains (climate Cw, according to the Köppen classification). This climate is characterized by a well-defined dry season in winter and spring, with a mean annual temperature of 10–20 °C and annual precipitation between 800 and > 2000 mm per year. In some parts of the eastern Sierra Madre and southern mountain systems, a small proportion of pine-oak forests can be found in the humid subtropical zone (climate Cf), a very humid area where it rains all year and there is not a well-defined dry season (Miranda and Hernández-X 1963; INEGI 2014). In this area mean annual temperature is 10–22 °C and an annual rainfall ranges between 800 and 4700 mm.

National Forest and soil inventory of Mexico
The study is based on the information obtained from the National Forest and Soil Inventory of Mexico, hereinafter INFyS. This inventory contains around 26,000 sampling units (conglomerates) homogeneously distributed throughout the country, following a rectangular grid with a distance between conglomerates that varies from 5 km in temperate regions to 20 km in arid zones (CONAFOR 2015). The INFyS follows a systematic scheme of stratified sampling, using conglomerates of plots as basic sampling units. The conglomerates are circular with
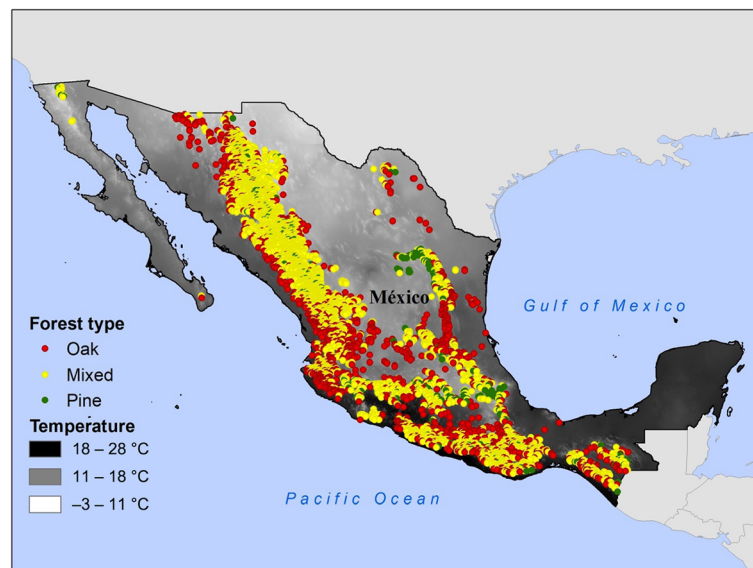
Fig. 1 Map of the study area showing the location of the 5458 conglomerates of the INFyS that were used to evaluate the regeneration of Pinaceae vs Fagaceae in Mexico. Sampling plots (dots) are overlaid on a mean annual temperature map. The colour of the dots represents the type of forest: oak-dominated overstory (red), pine-dominated overstory (green) or mixed pine-oak overstory (yellow)

56.42 m radius (1 ha). Each conglomerate contains 4 sub-plots of 400 m^2 each, 1600 m^2 per conglomerate in total, geometrically distributed in the form of an inverted "Y". We used the data from the inventories carried out in 2004–2009 (CONAFOR 2012) and 2009–2014 (CONAFOR 2018). The interval between the two inventories for a given sampling unit was on average 5 years but varied between 2 and 9 years depending on the conglomerate.

From all INFyS conglomerates we selected only those for which Pinaceae and/or Fagaceae species were present in at least one of the two inventories (2004–2009, 2009–2014). In addition, we only included conglomerates that met the following criteria: (i) the same plots had been measured (resurveyed) in the two inventories; (ii) total basal area was ≥ 2 m^2·ha^{-1} in the first survey so that very open forests were excluded; and (iii) did not contain human structures and roads and had not been severely affected by external impacts such as mining (according to INFyS surveys). Of all the conglomerates sampled in the INFyS, a total of 5458 met these criteria and were selected for this study. Only 517 plots (< 10%) were discarded for not meeting criteria (ii) and (iii) indicated above. Our analyses thus refer specifically to pine forests, oak forests and mixed pine-oak forests in a very broad sense, as determined based on the presence of overstory trees of the corresponding families according to INFyS surveys (see 'Stand characteristics' below). We note, however, that not all the natural distribution of these forest types in Mexico is included, as many of them were not sampled by INFyS or did not meet the previous selection criteria.

a) Stand characteristics At the conglomerate level, the following variables recorded in the INFyS surveys were included in our analyses: basal area (m^2·ha^{-1}) of all Pinaceae and Fagaceae species present (separately by family), total stand basal area (m^2·ha^{-1}), the occurrence of several disturbances, and land tenure (private; public, state owned; and social property, including the "ejido" and the communal properties). Overstory composition was determined according to the composition of the overstory (basal area of Pinaceae and Fagaceae species), and each conglomerate was classified in one of the following categories: Oak, for conglomerates where only Fagaceae were present in the overstory; Pine, for conglomerates were only Pinaceae were present in the overstory; and Mixed, for conglomerates where the two tree families were recorded in the overstory. We note that this classification may differ locally from standard vegetation types at the landscape level (e.g. those from INEGI (2014) vegetation maps). Nevertheless, we preferred to use a classification based on local, plot-level composition in our case, as in combination with the regeneration information analysed here provides richer and more accurate information on the likely population dynamics of the studied forests. Basal area measurements were averaged between the two INFyS surveys. Disturbance occurrence, including wildfires, grazing, pests and diseases, and wood extractions, was determined according to the information recorded during INFyS surveys. In these surveys,

the intensity of each disturbance was evaluated using a five-level ordinal scale. For simplicity, we reclassified these levels into two categories for each type of disturbance: low (no, barely noticeable or low impact in the two surveys) and high impact (medium or high impact as recorded in at least one of the surveys).

b) Regeneration of tree species Regeneration was sampled at the INFyS surveys as follows. At the center of each of the four sub-plots of 400 m^2 of each conglomerate, a circle of 12.56 m^2 (a total of 50.24 m^2 per conglomerate) was established where the regeneration was assessed. All individuals greater than 25 cm in height were considered as regeneration, up to the height they reached, provided that their diameter at breast height (DBH) was less than 7.5 cm. All individuals of each genus were counted and classified into three height classes: 25–150, 150–275 and > 275 cm. In this study, these height categories were reclassified into two classes: 25–150 cm height, which we called "saplings", and > 150 cm, which we called "small trees". Total Pinaceae and Fagaceae regeneration (individuals·ha^{-1}) were averaged between the two INFyS surveys for each conglomerate. By doing so we reduced the effect of temporal variability in regeneration on our results, which is particularly important considering that sampling years differed among conglomerates. The fact that we averaged the values from two inventories per conglomerate (instead of studying the changes between them) also implies that the effect of heterogeneous time intervals between surveys across conglomerates is likely to be negligible.

Climatic data

Bioclimatic variables were extracted from Worldclim (Hijmans et al. 2005), a free database of global climatic layers with a spatial resolution of approximately 1 km^2. The geographical coordinates of all conglomerates were superimposed to climatic layers using the ArcGis software to obtain the annual precipitation (mm) and the mean annual temperature (°C) of each conglomerate location.

Data analyses

The two response variables, sapling regeneration and small tree regeneration, had a large proportion of zeros (that is, conglomerates without regeneration of either saplings or small trees) (7.2% for saplings and 27.7% for small trees), and no transformation could satisfy the normality assumption. For this reason, each of these variables was analyzed in two steps. First, we transformed each variable to a dichotomous one, indicating the presence/absence of regeneration (of saplings or small trees) in each conglomerate. We used generalized, mixed-effects linear models with a binomial distribution and a
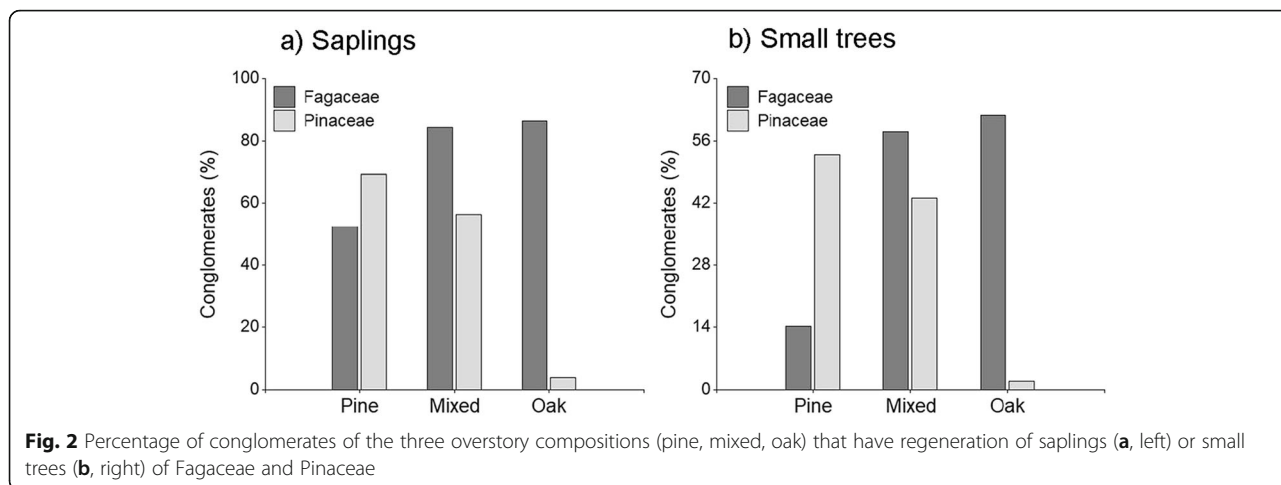
logit link function to analyze the presence of saplings and small trees (considered separately). As explanatory variables, we included the Family of the regeneration (Fagaceae, Pinaceae) and its interaction with: overstory composition (Oak, Mixed, Pine), total basal area (m^2·ha^{-1}) of the conglomerate, mean annual temperature (°C), annual precipitation (mm), land tenure (private, public, social), forest fires (low vs. high impact), grazing (low vs. high impact), pests and diseases (low vs. high impact), and wood extractions (low vs. high impact). We included Conglomerate nested in State ($N = 28$) as random factors. Conglomerate was included to account for the fact that data for the two families (Fagaceae, Pinaceae) was paired at the conglomerate level. State accounted for the effect of spatial autocorrelation at relatively large spatial scales (the average size of a Mexican state is 63,481 km^2), resulting for instance from differences in legislation or historical land-use between states.

In a second step, we used general, mixed-effects linear models to model regeneration abundance (of saplings or small trees) in conglomerates with at least one regenerating individual. As not all conglomerates had regeneration of the two families, we carried out four different linear models: two for saplings and small trees of Pinaceae, and two for saplings and small trees of Fagaceae. The explanatory variables were the same as in the models for regeneration presence except the family of the regeneration (and its interactions with the other variables), which could not be considered in this case. We again used mixed-effect models but in this case the only random effect was State. Regeneration abundance was log-transformed in all cases to satisfy normality assumptions. Some explanatory variables were also log- or square root-transformed, as indicated in the corresponding tables in the Results, to improve the distribution of model residuals. Stepwise model selection was applied starting from the saturated model and removing the least significant term until there was no further decrease in the Akaike Information Criterion (AIC). All statistical analyses were carried out with the R software (version 3.2.2, The R Foundation for Statistical Computing).

Results

Regeneration of Pinaceae and Fagaceae as a function of overstory composition

The presence of Fagaceae saplings was very common in the conglomerates with oak and mixed overstory, where the percentage of conglomerates with Fagaceae saplings was > 80% (Fig. 2). Half of the conglomerates with pine overstory had Fagaceae saplings (Fig. 2). On the other hand, Pinaceae saplings appeared in 69% and 56% of forests with pine and mixed overstory, respectively, but only in 4% of those with oak overstory. These patterns

Fig. 2 Percentage of conglomerates of the three overstory compositions (pine, mixed, oak) that have regeneration of saplings (**a**, left) or small trees (**b**, right) of Fagaceae and Pinaceae

were qualitatively similar, albeit with lower overall values, for small trees (Fig. 2).

Densities of Pinaceae and Fagaceae saplings and young trees (for the conglomerates showing regeneration) also varied depending on overstory composition (Fig. 3). Thus, Fagaceae saplings were more abundant than those of Pinaceae under the three overstory compositions, while those of Pinaceae had a particularly low density in forests with oak overstory (Fig. 3). On the other hand, small Fagaceae trees were more abundant than small pines in forests with mixed and particularly oak overstory, where small pines were basically absent (Fig. 3). Only in forests with pine overstory the densities of small pine trees were larger (approximately double) than those of small Fagaceae trees (Fig. 3).

Factors affecting the presence of saplings and small trees of Pinaceae and Fagaceae
Consistent with the previous results, the generalized linear mixed-effects model indicated that the presence of Fagaceae and Pinaceae saplings was higher under

canopies dominated by trees of their own family. Fagaceae presence was higher in forests with oak and mixed overstory, whereas saplings of the two families were similarly present in conglomerates with pine overstory (Table 1). Mean temperature had a positive effect on the presence of Fagaceae saplings but a strong negative effect on Pinaceae saplings (Fig. 4a, Table 1). The effect of precipitation was positive and similarly small for both families. Wildfires had a positive effect on the presence of Fagaceae saplings that was not observed for Pinaceae (Fig. 5a, Table 1); whereas the opposite occurred for grazing effects, which only affected (negatively) the presence of Fagaceae saplings (Fig. 6a, Table 1).

The overall patterns were similar when considering the regeneration of small trees (Table 1). The effect of temperature was not significant for Fagaceae, whereas it was again strongly negative for Pinaceae (Fig. 4b). On the other hand, the effect of precipitation was not significant for small trees (Table 1). The social land tenure was associated with higher presence of small Pinaceae trees, whereas this effect was not observed for Fagaceae.
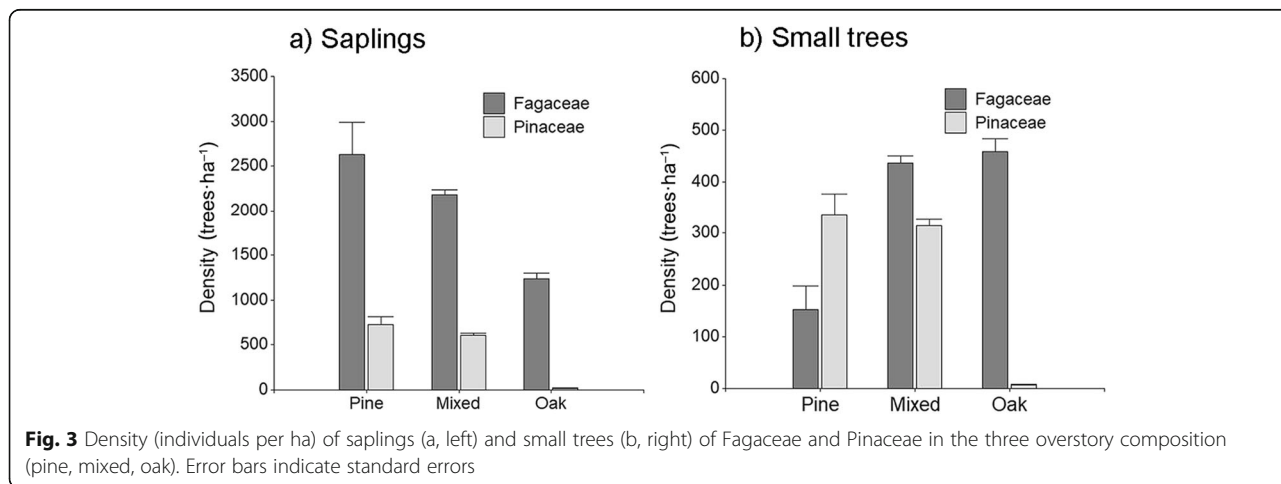

Fig. 3 Density (individuals per ha) of saplings (a, left) and small trees (b, right) of Fagaceae and Pinaceae in the three overstory composition (pine, mixed, oak). Error bars indicate standard errors

Table 1 Estimated coefficients (and corresponding standard errors, S.E.) of generalized linear mixed-effects models of the presence of saplings and small trees (binomial variable: yes, no) as a function of family (Fagaceae or Pinaceae), overstory composition (Overstory; oak, mixed or pine), total plot basal area (BA), climate variables (mean annual temperature and annual precipitation), occurrence of several disturbance types (wildfires, grazing, pests, wood extractions), land tenure (private, public or social), and the interactions between family and all the other variables

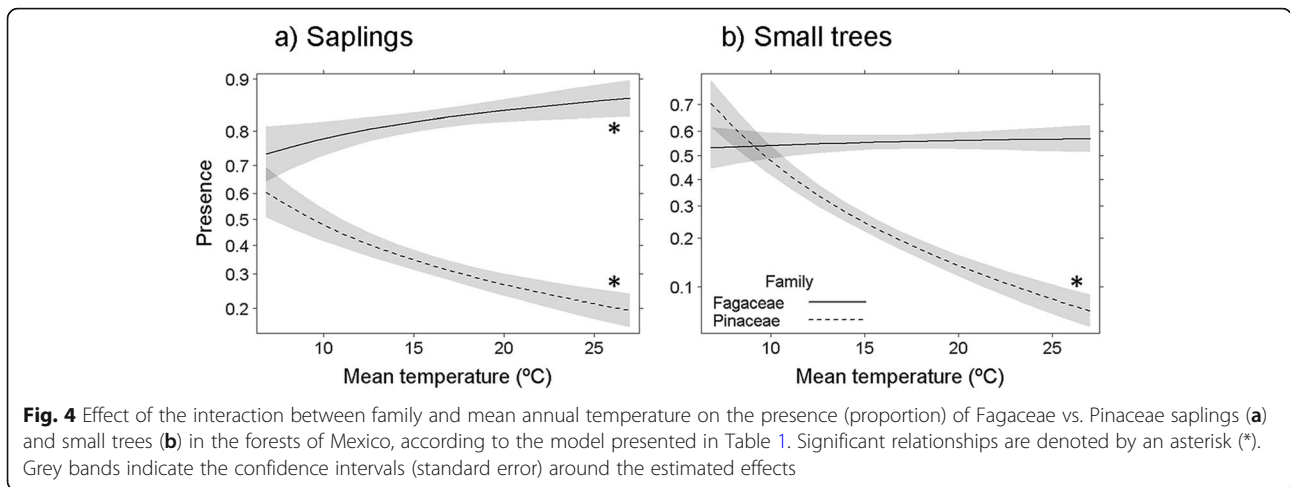| Variable	Saplings (Coef. ± S.E.)	Small trees (Coef. ± S.E.)
(Intercept)	−2.07 ± 0.90*	−0.03 ± 0.69
Family Pinaceae	− 0.08 ± 0.99	2.00 ± 0.89*
Overstory mxed	−0.30 ± 0.10**	−0.18 ± 0.08*
Overstory pine	−1.72 ± 0.16***	−2.30 ± 0.19***
sqrt (Total BA)	0.04 ± 0.04	0.04 ± 0.03
log (Mean temperature)	0.63 ± 0.24**	0.11 ± 0.19
log (Precipitation)	0.27 ± 0.14*	0.02 ± 0.11
Wildfires	0.54 ± 0.10***	0.01 ± 0.07
Grazing	−0.22 ± 0.09**	−0.23 ± 0.06***
Pests	0.09 ± 0.12	0.04 ± 0.09
Wood extractions	0.19 ± 0.11	0.05 ± 0.08
Land tenure Public	−0.65 ± 0.45	−0.15 ± 0.41
Land tenure Social	0.06 ± 0.09	−0.05 ± 0.07
Family Pinaceae: Overstory mixed	3.25 ± 0.18***	3.36 ± 0.22***
Family Pinaceae: Overstory pine	5.22 ± 0.26***	5.64 ± 0.31***
Family Pinaceae: sqrt (Total BA)	0.04 ± 0.06	0.07 ± 0.05
Family Pinaceae: log (Mean temperature)	−1.97 ± 0.29***	−2.63 ± 0.26***
Family Pinaceae: log (Precipitation)	0.08 ± 0.17	0.09 ± 0.15
Family Pinaceae: Wildfires	−0.57 ± 0.12***	−0.39 ± 0.10***
Family Pinaceae: Grazing	0.24 ± 0.11*	0.44 ± 0.10***
Family Pinaceae: Pests	0.04 ± 0.16	0.22 ± 0.13
Family Pinaceae: Wood extractions	0.22 ± 0.14	0.20 ± 0.12
Family Pinaceae: Land tenure Public	0.98 ± 0.65	0.42 ± 0.65
Family Pinaceae: Land tenure Social	0.09 ± 0.12	0.24 ± 0.11*

Coefficient values are given relative to the reference level for each factor-type variable (Family = 'Fagaceae', Overstory = 'Oak', Land tenure = 'Private', and no/low disturbance level for all disturbance types), which implies that the estimate for the reference level of each factor is included in the intercept, and the coefficients for the additional (non-reference) factor levels indicate how they deviate from the overall intercept. The same applies to interactions with family: the coefficients corresponding to each of the other explanatory variables (without interaction) correspond to their estimated effect for Fagaceae (the reference level for family), whereas the bottom 11 rows show how this effect is modified for Pinaceae species. Conglomerate nested in state were included as random factors. Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. Significance codes: * $0.05 < P < 0.01$; ** $0.01 < P < 0.001$; *** $P < 0.001$

Wildfires had a negative effect on the presence of Pinaceae small trees, whereas the effect was neutral for Fagaceae (Fig. 5b, Table 1). Grazing was associated with higher presence of small Pinaceae trees and lower presence of small Fagaceae trees (Fig. 6b, Table 1).

Factors affecting the abundance of saplings and small trees of Pinaceae and Fagaceae

Overstory composition had a significant effect on the general linear mixed-effects models carried out for the abundance of the saplings of the two families separately. Density of both Pinaceae and Fagaceae saplings was higher in forests with mixed and pine overstory than in

those with oak overstory (Table 2, see also Fig. 3). Basal area contributed positively to the abundance of Pinaceae saplings but negatively to that of Fagaceae (Table 2). Concerning climatic factors, temperature negatively affected the abundance of saplings of both families, although the effect was stronger for Fagaceae, while precipitation had always a positive effect (Table 2). Wood extractions increased the abundance of Pinaceae saplings only, whereas fires had a positive effect and grazing a negative effect on the abundance of Fagaceae saplings only (Table 2). Finally, the social tenure of the land was associated to higher abundance of Pinaceae saplings.

Fig. 4 Effect of the interaction between family and mean annual temperature on the presence (proportion) of Fagaceae vs. Pinaceae saplings (**a**) and small trees (**b**) in the forests of Mexico, according to the model presented in Table 1. Significant relationships are denoted by an asterisk (*). Grey bands indicate the confidence intervals (standard error) around the estimated effects
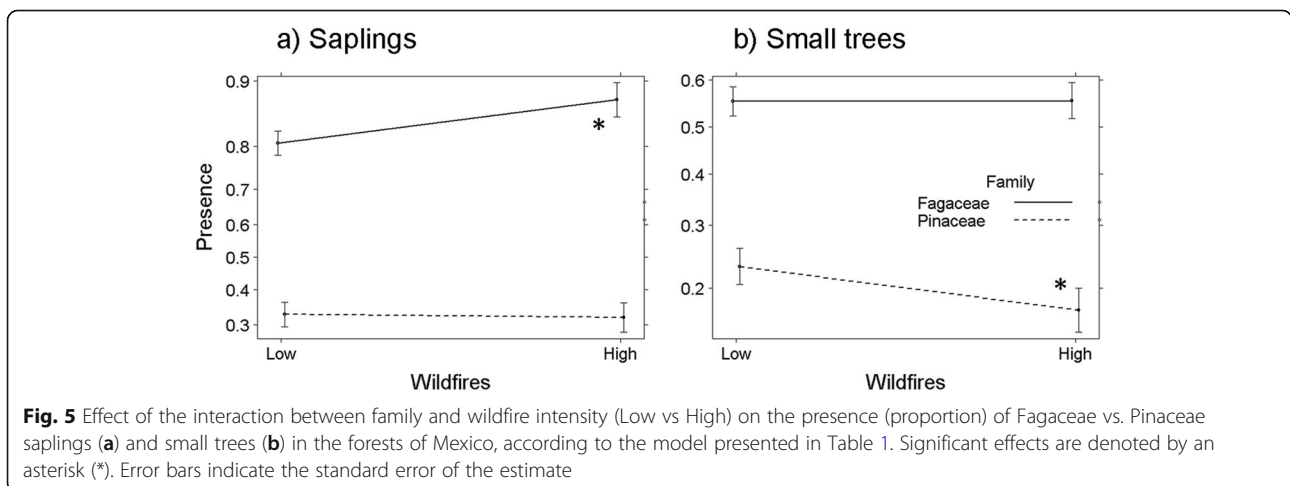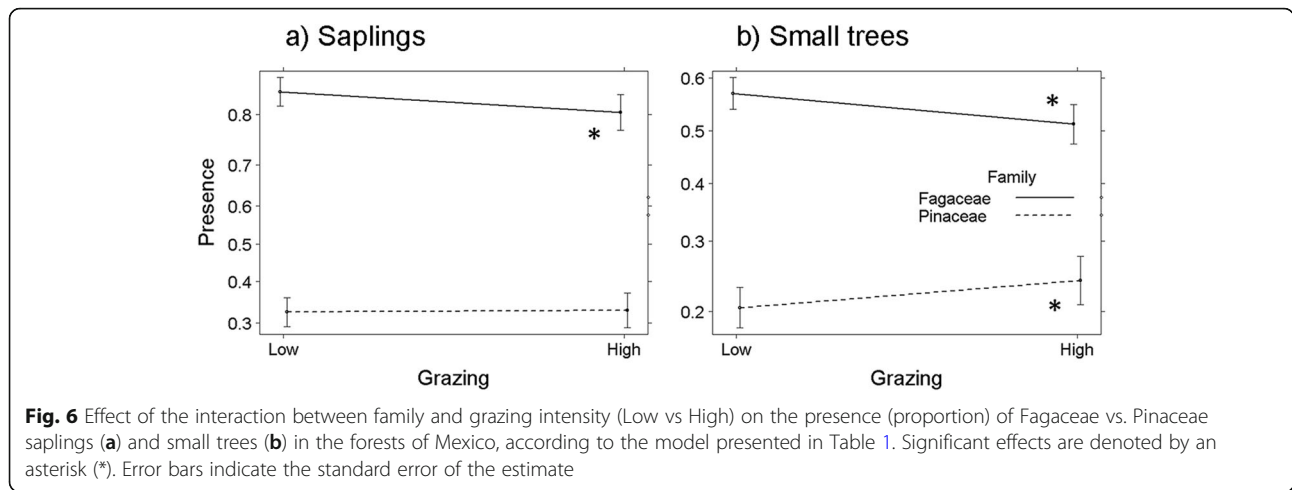
In the general linear mixed-effects models for the abundance of small trees the effect of overstory composition was not significant for either of the two families (Table 2). As in the case of the sapling models, basal area contributed positively to the abundance of small Pinaceae trees but negatively affected that of Fagaceae (Table 2). Temperature negatively affected the abundance of both families, while precipitation had a positive effect on the abundance of small Pinaceae trees only. As far as disturbances are concerned, fires were associated with higher abundance of small Fagaceae trees and had a negative effect on Pinaceae, while grazing was associated to lower abundance of small Fagaceae trees only (Table 2). Finally, the abundance of small Fagaceae trees was higher under social tenure, but this effect was not observed for Pinaceae.

Discussion

Our results show that regeneration patterns in pine-oak Mexican forests differ substantially between Pinaceae and Fagaceae, with regeneration of Fagaceae tending to dominate over that of Pinaceae in forests with oak and mixed overstory. We acknowledge that this outcome and the other results reported here need to be interpreted with caution, as the information provided by the INFyS is relatively coarse, as in any nationwide forest inventory, and may not be accurate enough to characterize detailed ecological patterns, particularly at local scales. However, nationwide forest inventories remain an unvaluable source of information to assess regeneration patterns at regional scales or broader, and hence we restrict our discussion to general patterns and associations identified at the country scale. The fact that, overall, saplings and small trees of Pinaceae and Fagaceae were generally more abundant under canopies dominated by trees of their own family and in mixed forests than in forests dominated exclusively by the other family indicates that regeneration is largely determined by overstory composition. This does not support the expected greater shade tolerance of Fagaceae relative to Pinaceae species, and

Fig. 5 Effect of the interaction between family and wildfire intensity (Low vs High) on the presence (proportion) of Fagaceae vs. Pinaceae saplings (**a**) and small trees (**b**) in the forests of Mexico, according to the model presented in Table 1. Significant effects are denoted by an asterisk (*). Error bars indicate the standard error of the estimate

Fig. 6 Effect of the interaction between family and grazing intensity (Low vs High) on the presence (proportion) of Fagaceae vs. Pinaceae saplings (**a**) and small trees (**b**) in the forests of Mexico, according to the model presented in Table 1. Significant effects are denoted by an asterisk (*). Error bars indicate the standard error of the estimate

likely reflects the diversity of shade tolerance attributes within families, especially among the pines (McCune 1988; Retana et al. 2002).

Climate is an important determinant of successional dynamics of pine-oak species in Mexico (Roncal-García et al. 2008; van Zonneveld et al. 2009; Figueroa-Rangel et al. 2012). Importantly, our results suggest that the effect of climate differs between families, as warm

temperatures benefited the presence of saplings and, to a lesser extent, the presence of small trees of Fagaceae, but strongly reduced the presence of saplings and small trees of Pinaceae. This result can have important implications under ongoing climate warming and the corresponding increase in the frequency and intensity of hotter droughts, which has already been reported in central America (Margolis et al. 2017). As expected,

Table 2 Estimated coefficients (and corresponding standard errors) of general linear mixed-effects models of the abundance of Pinaceae and Fagaceae saplings and small trees (separate models for each combination) as a function of overstory composition (Overstory; oak, mixt, pine), total plot basal area (BA), climate variables (mean annual temperature and annual precipitation), occurrence of several disturbance types (wildfires, grazing, pests, wood extractions), land tenure (private, public or social), and the interactions between family and all the other variables

Variable	Saplings		Small trees	
	Pinaceae	Fagaceae	Pinaceae	Fagaceae
	Coef. ± S.E.	Coef. ± S.E.	Coef. ± S.E.	Coef. ± S.E.
(Intercept)	2.50 ± 0.66***	7.56 ± 0.50***	4.93 ± 0.66***	7.72 ± 0.34***
Overstory Mixed	0.58 ± 0.15***	0.17 ± 0.05***	–	–
Overstory Pine	0.61 ± 0.17***	0.54 ± 0.11***	–	–
sqrt (Total BA)	0.07 ± 0.03*	− 0.07 ± 0.02***	0.11 ± 0.03***	− 0.08 ± 0.02***
log (Temperature)	−0.38 ± 0.17*	−0.99 ± 0.13***	−0.65 ± 0.16***	−0.53 ± 0.11***
log (Precipitation)	0.54 ± 0.09***	0.31 ± 0.07***	0.35 ± 0.09***	–
Wildfires	–	0.30 ± 0.04***	−0.14 ± 0.06*	0.12 ± 0.04**
Grazing	0.08 ± 0.05	−0.25 ± 0.04***	–	− 0.10 ± 0.04**
Pests	–	–	–	–
Wood extractions	0.14 ± 0.06*	−0.09 ± 0.05	–	–
Land tenure Public	0.49 ± 0.32	–	–	−0.04 ± 0.25
Land tenure Social	0.13 ± 0.06*	–	–	0.10 ± 0.04*
R^2 marginal	0.054	0.059	0.045	0.022
R^2 conditional	0.107	0.111	0.085	0.083

Coefficient values are given relative to the reference level for each factor-type variable (Overstory = 'Oak', Land tenure = 'Private', and no/low disturbance level for all disturbance types), which implies that the estimate for the reference level of each factor is included in the intercept, and the coefficients for the additional (non-reference) factor levels indicate how they deviate from the overall intercept. State was included as a random factors (see text). Model selection was based on AIC. Some variables were log- or square-root (sqrt) transformed to ensure normality, as indicated below. Significance codes: * 0.05 < P < 0.01; ** 0.01 < P < 0.001; *** P < 0.001

precipitation generally benefited the regeneration of both families. In northern Mexico, the highest peaks of pine and oak regeneration have been associated with unusually wet and fire-free periods (Meunier et al. 2014).

Our results show that disturbances also determined regeneration patterns and had differential impacts between families. Although disturbance effects have to be interpreted with caution, because they rely on punctual information recorded exclusively during INFyS surveys, our models suggest that forest fires reduced the presence and abundance of Pinaceae regeneration relative to Fagaceae. This general result certainly masks large variability in fire impacts on regeneration depending on fire regimes (Fulé and Covington 1998) and local conditions (climate, dominant species; Rodríguez-Trejo and Fulé 2003). However, the fact that our results were highly consistent among regeneration classes (saplings vs. small trees) and for both the presence and abundance of regeneration (Tables 1 and 2) gives us confidence on the strength of this result at the country scale.

In the second half of the twentieth century fire regimes changed drastically in many Mexican temperate forests, which has caused long periods without fires, promoting a greater recruitment of coniferous species, as well as a large accumulation of igneous fuels (Minnich et al. 2000; Rodríguez-Trejo and Fulé 2003; Cortés Montaño et al. 2012). This accumulation of fuel has promoted large forest fires in some areas, which are known to promote oak woodlands and shrublands over pine forests (Barton and Poulos 2018). The predominance of oak species in post-fire stands is favoured by their sprouting capacity after disturbance (Fulé and Covington 1998; Aguilar et al. 2012; Stambaugh et al. 2017). In addition, *Quercus* species have deep root systems that help them prevent water stress, which may be advantageous in the dry, post-fire conditions (Davis and Mooney 1986; Anderegg et al. 2015). In contrast, relatively few Mexican pine species have specific mechanisms to cope with fires and establish themselves after a large fire, such as a thick bark, serotine cones or resprouting capacity (Rodríguez-Trejo and Fulé 2003).

Besides wildfires, livestock grazing was the disturbance recorded in this study that was associated to greater differences between Fagaceae and Pinaceae regeneration. The strong negative impact of grazing on the presence and abundance of seedlings and small trees of Fagaceae, which was not observed for Pinaceae, can be explained by the lower palatability and generally higher tolerance to browsing of pines (Wahlenberg et al. 1939; Hernández et al. 2000). Differential human management and use of these two species groups may also contribute to explain the observed regeneration patterns, as acorn consumption, trampling and browsing of the young shoots cause a strong reduction in the establishment and

growth of oaks in browsed areas (Quintana-Ascencio et al. 2004; Hernández et al. 2000). The importance of management and land use is consistent with previous reports (Heyerdahl and Alvarado 2003; García-Barrios and González-Espinosa 2004; Works and Hadley 2004) and with the effect of land tenure in our results, suggesting that the abundance of Pinaeae saplings and small Fagaceae trees may be favored under a social tenure. Although wood extractions had a relatively small effect in our models, 75% of timber extractions in Mexico correspond to pine species (Segura 2000), which should have strong effects on regeneration patterns and stand dynamics. In addition, we acknowledge that other factors not included in our analyses affect regeneration success and likely contribute to the observed differences between families.

Factors related to stand structure and development also affected the regeneration of pine-oak forests in Mexico. The abundance of Pinaceae was favored in high basal area stands, while the abundance of Fagaceae saplings and small trees was negatively affected by total basal area. These results challenge the view that Pinaceae tend to be more early-successional than Fagaceae. However, they are consistent with several studies reporting that colonization of broadleaf species is low in mature, high basal area forests dominated by Pinaceae (Camacho-Cruz et al. 2000; Ramírez-Marcial et al. 2001; Galindo-Jaimes et al. 2002; Alba et al. 2003; García-Barrios and González-Espinosa 2004; Ramírez-Marcial et al. 2006). As already mentioned, within-family diversity in shade tolerance is high and oak regeneration may require the presence of open spaces upper in the tree canopy (Stambaugh et al. 2002; López-Barrera et al. 2006; Pérez et al. 2013), which are dependent on specific disturbance regimes (González-Espinosa et al. 1991; Galindo-Jaimes et al. 2002; Quintana-Ascencio et al. 2004; Meunier et al. 2014).

Conclusion

Overall, our results show that in Mexican forests the regeneration of Fagaceae tends to dominate over that of Pinaceae, although this depends on overstory composition and disturbance regime. The fact that Fagaceae regeneration seems to be favoured, relative to Pinaceae, under warmer climates and in the presence of wildfires, suggests that ongoing climate change (Sáenz-Romero et al. 2010) could favour the predominance of oaks, particularly in drier areas (Melo et al. 2010; Meunier et al. 2014). These changes are consistent with global patterns reported for global temperate forests (Alfaro-Reyna et al. 2018) and with current growth trends in Mexican forests (Alfaro-Reyna 2019). Although the final outcome will critically depend on human management and land use, the

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structure, composition and functioning of many Mexican pine-oak forests could be strongly modified (Gómez-Mendoza and Arriaga 2007; Gómez-Mendoza et al. 2008; Galicia et al. 2013). This would also have an important socioeconomic impact, due to the key role of Mexican pine-oak forests as providers of ecosystem services (Segura 2000) and the fact that many local communities depend directly on forest products for their subsistence (FAO 2010). Further research assessing mid-term temporal dynamics is needed to confirm the trends reported in this study, as well as to provide more detailed understanding of the corresponding spatial patterns and the implications for forest resilience under future disturbance regimes.

Ethical approval and consent to participate
Not applicable.

Authors' contributions
TA, JR and JMV conceived the study and planned the work. TA prepared the dataset and lead data analysis and manuscript writing with active participation from JR and JMV. All authors read and approved the final manuscript.

Availability of data and materials
Data will be made available on demand.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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